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SOME CASES OF PLANTS SUPPRESSED BY OTHER PLANTS.

BY C. A. M. LINDMAN (Stockholm).

[WITH PLATE I AND ONE FIGURE IN THE TEXT].

I.

EVERY botanist is well acquainted with the fact that certain plants of considerable size and dense growth exercise an influence disadvantageous to much of the accompanying flora: the deep shade cast by such plants prevents many species from attaining a normal development and finally kills them. The common nettle for instance, *Urtica dioica*, is able to suppress other plants entirely, so that if a large *Urtica*-group is cut away, there will be seen no other vegetation on the central parts of the area occupied by the nettles, the soil being quite bare. The International Phytogeographical Excursion in the British Isles (1911) visited the woods in the neighbourhood of Honley, Yorks., and the party had the opportunity of admiring the gigantic form of *Pteridium aquilinum*, widely distributed in shady woods on the slate, and differing from the dwarf form on siliceous grasslands.[1] *Pteridium* also is a plant which grows so densely that it may exclude all herbs and grasses. I have seen the same species in South Brazil, where it forms enormous thickets very much higher than in Britain (leaves are met with 6 to 7 m. long; at Honley I saw leaves 2 m. long.) In Brazil, however, this fern grows abundantly, chiefly in sunny places where the forest has been destroyed[2], and consequently it has there not quite the same biotic influence as in the British woods just mentioned, where it belongs to the shade ground vegetation.

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[1] See T. W. Woodhead, "Ecology of Woodland Plants." Journ. Linn. Soc., Bot., 1906, p. 368; also A. G. Tansley, "Types of British Vegetation," 1911, Plate 1.

[2] Mentioned by P. W. Lund in 1835, and E. Warming in "Lagoa Santa," 1892, &c.

A well-known example of the same kind is the suppressing effect which the beech (*Fagus silvatica*) and the spruce (*Picea*), both of which constitute very dark forests, exercise on the oak. In Germany and in South Sweden the oak, *Quercus robur*, eventually yields to the beech; and in Central Sweden (*e.g.* at Stockholm) isolated old and nearly ruined oaks are met with in the pure spruce woods, where, for want of daylight, no oak seedlings are nowadays seen.

There is, however, another European forest-tree, the shade of which is still more intense than that of the beech. This is the yew (*Taxus*), of which the largest and purest wood in the British Isles, the famous wood of Kingley Vale (Sussex), was shown to the foreign members of the International Excursion, and caused their enthusiastic admiration. In this yew wood the ground was to a great extent entirely bare,[1] without any vegetation, phænogamous or cryptogamic, consisting only of a dark brown earth, and never reached by any sun glimpse. There is evidently in the British flora no species able to settle and form a ground vegetation in darkness like this. In the tropics, *e.g.*, South Brazil, the darkest woods and groves never lack a dense ground vegetation of miniature trees, ferns, and a few herbs.[2]

Plate I, Fig. 1 shows two individuals of *Taxus* at the margin of the large yew wood at Kingley Vale; one of these (to the left) is seen behind a large juniper, in the faint shade of which the yew has germinated. Later on, the juniper will be hidden, suffocated and killed by its neighbour, as has already happened with the junipers beneath the larger yew to the right. There is hardly a stronger contrast in British nature, in regard to the available light, than that between the black interior of the pure, dense yew wood and the complete exposure on the bright southern slope of a chalk down.

II.

I shall now call attention to a herbaceous plant, which, even when present as isolated individuals, is able to suppress its nearest neighbours by the shade of its leaves, together with the direct contact and pressure. This is *Hypochœris maculata*. In Great Britain it is recorded from the chalk and limestone; on similar habitats in Sweden it generally occurs in a dwarf form with small deeply cut leaves. But on the siliceous and granitic ground of Central Sweden it grows very tall and produces radical leaves up to 20 cm. long and 8 cm. broad. On dry hill-sides and on the borders of pine woods, in close short pasture on sandy or loamy drifts (old ground moraines), this species is sometimes numerous, the large radical leaves all horizontally expanded, and the large flat rosette pressed to the ground. It is evident that all small and weak plants beneath such a rosette would be pressed down and kept in obscurity during 4—5 months.

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[1] See also A. G. Tansley, "Types of British Vegetation," p. 170.

[2] I have endeavoured to sketch this in the book, "Vegetation in Rio Grande do Sul," 1900, pp. 130, 163.

The herbaceous vegetation of these localities is poor, more rarely a fairly good pasture, consisting chiefly of *Potentilla erecta*, *P. verna*, *Veronica officinalis*, *Campanula rotundifolia* (a tiny form), *Leontodon autumnalis*, *Luzula campestris*, *L. multiflora*, *Agrostis vulgaris*, *Festuca ovina*, &c. Although the rosette leaves of *Hypochœris maculata* are not very firm, all the plants mentioned succumb to the pressure and the shade, and it is curious to see how below a *Hypochœris*-rosette there are only tiny, etiolated shoots or bare soil. Several plants, however, save themselves by a long creeping stem, which does not suffer at all when the base is covered, e.g., *Potentilla erecta* and *Veronica officinalis*, and others (*Campanula rotundifolia*) by short runners or stolons; but many herbs and all mosses and lichens are suppressed by the large-leaved *Hypochœris*. In somewhat shady places where *Dactylis glomerata*, *Melampyrum nemorosum*, *Ranunculus acer*, *R. polyanthemus*, *Silene nutans*, *Galium boreale*, *Festuca elatior*, *F. rubra*, *Trifolium medium*, &c., are growing (the examples are chosen from the vicinity of Stockholm), the basal leaves of *Hypochœris* are not able to do any harm, as they are forced into an upright position.

III.

One of the most striking examples of a herbaceous plant possessing an irresistible power to force away and displace the accompanying plants in the same association by means of strong growth and firm stiff leaves, is *Juncus squarrosus*. This species was seen abundantly on high-lying dry plateaux and slopes in northern England and Scotland during the International Phytogeographical Excursion, 1911.

Many of the members of the Excursion will remember it. On the grit grassland at the higher levels of Crossfell in Westmoreland (Text-Fig. 1), on the immense, slightly inclined slopes of Ben Lawers (Plate I, Fig. 2), and in several other places.

The British form met with in the dry, hot summer of 1911 was

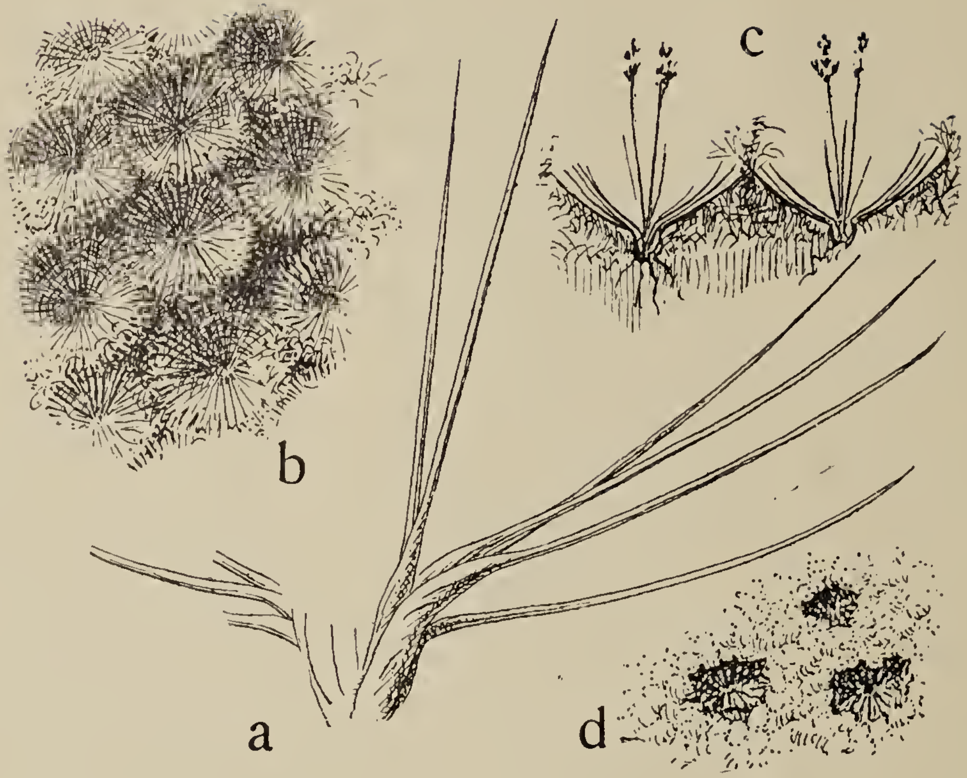

Fig. 1. *Juncus squarrosus* (Crossfell, Aug. 13th). *a*, some of the basal leaves (about half natural size); *b*, a group of rosettes seen from above, the interspaces filled up by *Agrostis vulgaris*; *c*, two individuals in vertical section (schematic); *d*, some rosettes in a *Sphagnum* bed nearly shut up,

very short and coarsely growing, the rosette leaves only 10—12 cm. long. The species occasionally produces leaves 20—30 cm. long. As it was observed rather late in the year (August), and with ripe fruits or nearly so, its most peculiar feature, the spreading leaves, was very distinctly developed.

In fact, this peculiar manner of growth attracted the attention of many of the party. Having made some notes on the subject and some schematic drawings, I asked my companions whether there was any record of this matter. Nobody had any knowledge of such observations, nor have I later found anything published on the singular behaviour of *Juncus squarrosus* to the surrounding vegetation. I therefore now give a short account of the action of this plant in suppressing other herbs and grasses of its habitat.

Where *Juncus squarrosus* occurs abundantly, it seems to cover the ground entirely (see Plate I, Fig. 2). It occupies great areas, and I saw places where I could walk a hundred yards in a straight line without seeing any interruption in the apparently pure " Juncetum squarrosi."

At the same time the plant differs from its neighbours by forming, not a smooth continuous lawn or carpet, but a rough pasture, where each individual rosette (more correctly each plant composed sympodially of several axillary rosettes) has the shape of a shallow cup or of a bird's nest (Text-Fig. 1, *b*, *c*), in the centre of which the leafless stem arises. A single individual (*viz.*, the flowering stem, sometimes two or three together, with the—simple or compound—rosette) has generally about twenty green leaves, or even twice as many, besides the dead brownish ones from the preceding year. All these leaves are bent outwards at the very base (Fig. 1, *a*), as soon as they become full-grown. In June and July there are still young, soft leaves in the middle, standing up close to the inflorescence; but in August they are all spreading rigidly outwards.[1] They spread at an angle of 40—90° to the perpendicular and force away all the surrounding herbs and grasses, except the adjoining rosettes of the same species, for every time *Juncus squarrosus* was seen in great numbers and the rosettes adjoined each other, they were all of the normal size (a diameter of about 1 dm.), and the distance from centre to centre is the same as the diameter of a rosette (Fig. 1, *b*).

Owing to the considerable number and thickness of the blades, the bottom and sides of the "cup" or "nest" are quite impermeable to the shoots of other plants.

In dense colonies of *J. squarrosus* there will be very little space left for other herbaceous plants. On Crossfell the commonest plant accompanying *J. squarrosus* was *Agrostis vulgaris* (*A. tenuis* Sibth. ?), a tender form with narrow leaves. This plant has but little ability to resist the pressure of the *Juncus*, and where the latter was growing densely, the *Agrostis* appeared as thin vertical layers, jammed in between the rosettes of the *Juncus* (Fig. 1, *b*, *c*) and scarcely overtopping its leaf points. As the *Juncus* leaves partly keep green and fresh in the winter and do not lose their form and firmness after withering, the *Agrostis* has no chance to recover its lost position. In fact, below and between the *Juncus* rosettes there is a soft mass of withered *Agrostis* leaves, but this plant now produces numerous axillary shoots higher up on the stem than usual. It is thus evident that *Juncus squarrosus* would fail to get air and light enough, were it not able to keep its rosette open by means of the rigidly spreading leaves.

Other species which grow with *J. squarrosus* on Crossfell, and are caught and suppressed in the same way as *Agrostis vulgaris*, are *Deschampsia flexuosa*, *Festuca ovina*, *Galium saxatile*, *Vaccinium*

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[1] The anatomical structure is figured in Raunkiaer's "De Danske Blomsterplanters Naturalhistorie," **1**, 1895—99, p. 407, fig. 194, D; and Kirchner, Loew and Schroeter's "Lebensgesch. d. Blütenpflanzen Mitteleuropas," Lief. 10, 1909, p. 104, fig. 61.

myrtillus (the dwarf form of the hills in northern England), *Polytrichum* sp. (without sporangia), *Dicranum* sp., a few other mosses, and *Cladonia rangiferina.* More rarely this was the case with *Nardus stricta.* On Ben Lawers even the predominant, firm and rigid *Alchemilla alpina* was shut up and flattened, where the rosettes of *J. squarrosus* occurred densely (see Plate I, Fig. 2).

Only in *Sphagnum* does *Juncus squarrosus* seem to succumb. I once saw these two together (Crossfell); the *Juncus* was sunk rather deeply in the wet *Sphagnum* bed, and this grew freely over the leaf points of the rosettes. Consequently the *Sphagnum* was able to shut up the rosettes (as seen in Fig. 1, *d*), and on account of the peculiar consistence and nearly amorphous growth of the moss bed, it is not likely that it would be forced back by the spreading *Juncus* leaves.

Of herbaceous plants there are indeed very few that constitute such an effective biotic factor as *J. squarrosus*, unless they have strong mechanical resources for the struggle against plants of the same size. A similar effect we may of course expect in the case of woody plants, which in fact very often become predominant in various associations other than scrub and woodland. In the British Isles there are good examples in *Ulex europæus* and *U. Gallii* on heaths and pastures, *Vaccinium myrtillus*—together with *Rubus chamæmorus*—on the "peat hags" of the Pennines, &c. As regards *Juncus squarrosus*, there is no doubt that, although it is very much eaten by sheep, it will proceed in its conquest of the upland pastures, as long as the climatic conditions are favourable.

DESCRIPTION OF THE PHOTOGRAPHS ON PLATE I, ILLUSTRATING PROF. LINDMAN'S PAPER ON "PLANTS SUPPRESSED BY OTHER PLANTS."

Fig. 1. Yews and Junipers at Kingley Vale, illustrating the suppression of Juniper by Yew. Phot. W. B. Crump, 1911.

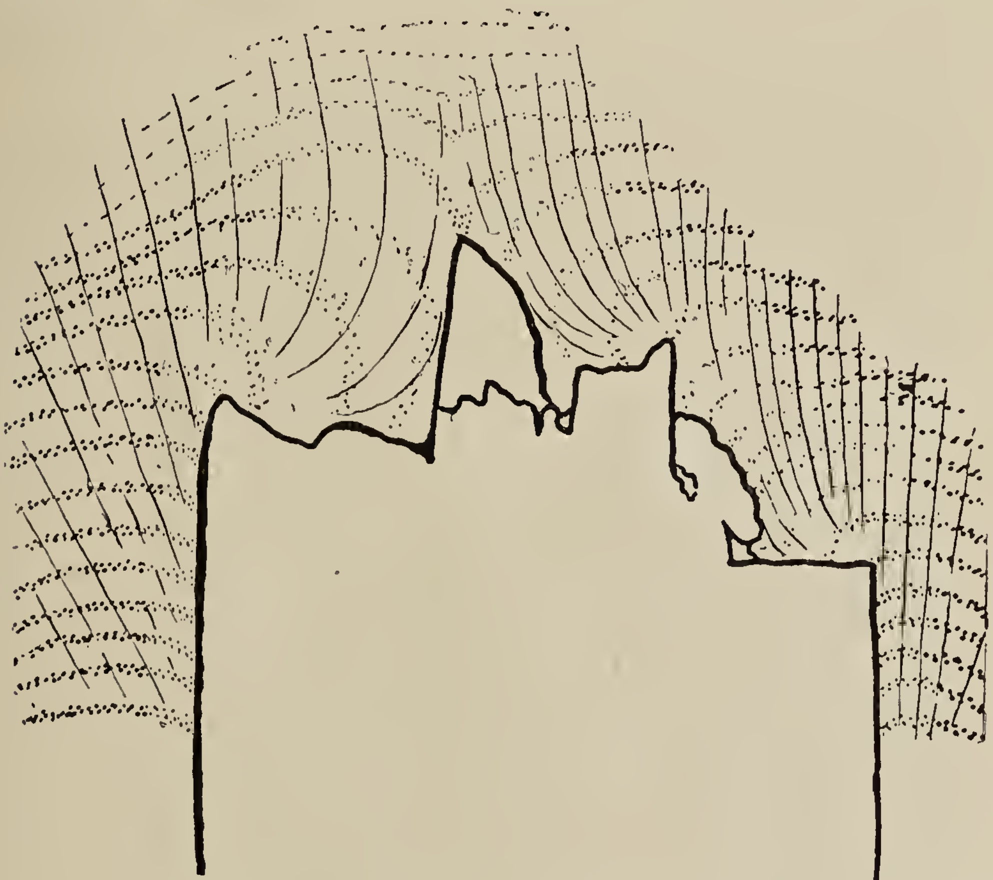
Fig. 2. *Juncus squarrosus* on Ben Lawers: several plants forming a pure clump in association of *Alchemilla alpina*. Phot. J. Massart, 1911.

SOME OBSERVATIONS ON WOUND HEALING IN A SPECIES OF OAK.

By A. V. Duthie.

[With Plate II and Three Text-Figs.]

THE slab of oak under consideration was sent to Professor Seward by Mr. Sindall of Cambridge. The wood is stated to be Austrian oak and from its general appearance and structure probably belongs to the species *Q. pedunculata.* Assuming that a single ring was produced each year the trunk must have been 160 years old when felled, with a diameter of 37cm. The ten outer rings, which belong to the sap-wood, are much lighter in colour than the heart-wood, and the limit between the two is made still more evident to the naked eye by a dark brown border due to the presence of tanniniferous contents in the cells of the wood-parenchyma and medullary rays (Plate II, Figs. 1 and 2).



Text-Fig. 1. Outer jagged end of embedded deal peg showing occluding callus layers.

The tree from which the slab was sawn received numerous wounds at different periods of its growth. The most striking of these is due to the insertion of a deal peg when the tree was 112 years old (Plate II, Fig. 1). The wood was morticed out to the depth of about 13 cm., and the peg, which is 6½ cm. thick and 22 cm. long, was driven in, leaving about 13 cm. projecting from the wound. This projecting portion was completely covered over in 38 years. The effect of the injury is observable in the widening of the annual rings to a lateral distance of over 5 cm. from the wound. The average breadth of the rings formed immediately before the injury is under 3 mm., the greatest breadth (12 mm.) is reached in the second year after wounding. From this point the breadth of the successively formed rings of wood decreases, until after 9 years from the injury the breadth of about 3 mm. is once more attained.

As the callus lips arch over the jagged end of the deal peg they broaden once more (Fig. 1), pushing into every crevice and coming into close contact with its irregular surface. A considerable amount of cortical tissue was formed in the callus-cushions before their coalescence; this is easily recognised by the brownish appearance of the tissues lying next to the peg and the interspersed groups of sclerotic cells. Owing to the pressure exerted by the fusing callus lips the arrangement of tissues is in this region much confused, groups of bark and wood elements being intermingled.

The callus wood which has closed over the end of the embedded peg shows in a very marked degree the phenomenon known as "speckled" or "curled" grain.[1] The large medullary rays as seen in tangential section do not exhibit the usual narrow elliptical form but are broadly oblong, triangular or circular in outline; while the course of the wood elements is much twisted (Plate II, Fig. 3). This peculiarity of structure is due in part to the jagged nature of the surface covered over by the callus and in part to the formation of adventitious buds, two of which are shown in transverse section in Plate II, Fig. 3.

In six of the remaining seven wounds exhibited by the specimen the outer tissues alone have perished and healing by occlusion has resulted. The injuries occurred in the 50th, 61st, 63rd and 113th years of growth. The area of wood laid bare by these wounds varied in extent and the healing process occupied from two to five years according to the extent of the injury. In the largest wounds examined the exposed wood has undergone considerable decomposition, and fungus spores and mycelial threads were noticed. In other cases the exposed wood is perfectly sound and has been effectually protected against decay by the formation of tyloses and the impregnation of the walls with tannin.

[1] Frank. Krankheiten der Pflanzen, I, p. 80.

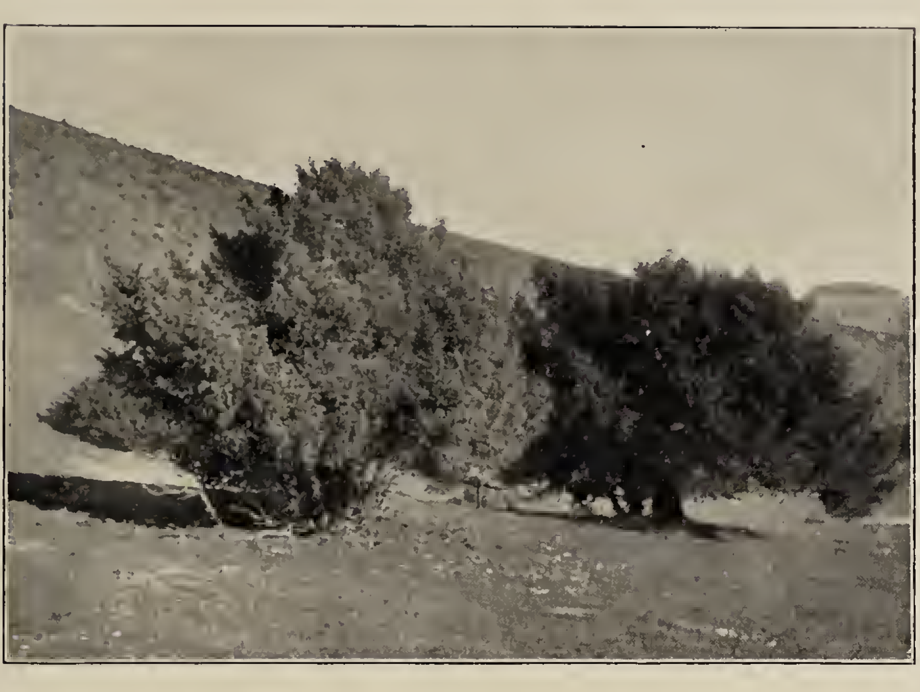


Fig. 1.

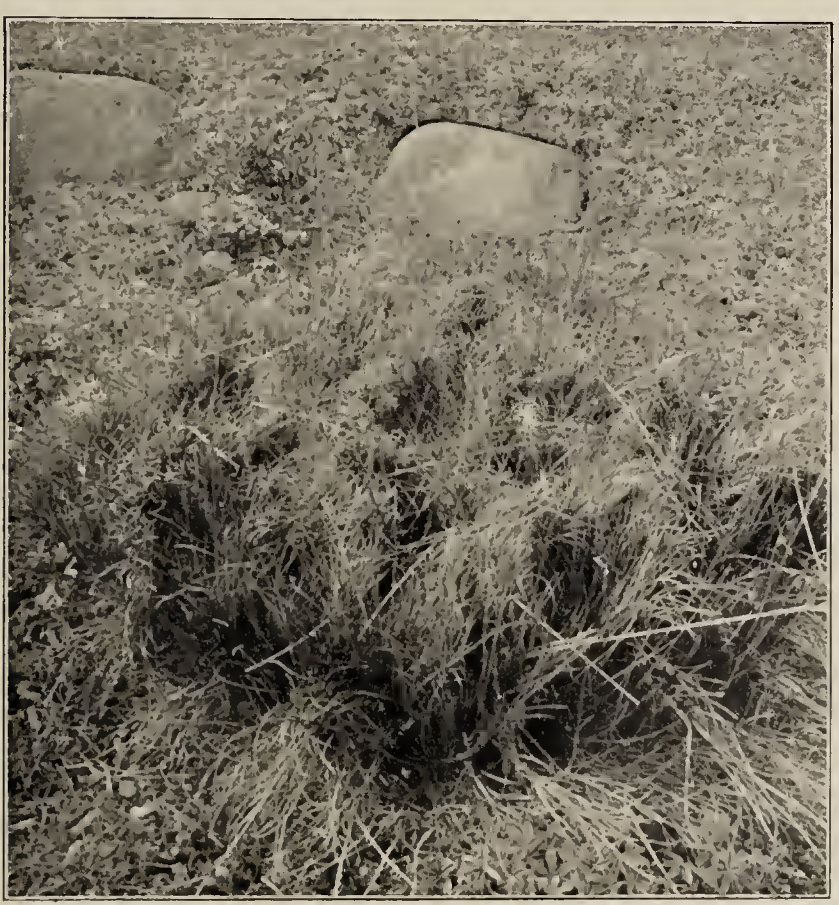


Fig. 2.

LINDMAN.—PLANTS SUPPRESSED BY OTHER PLANTS.

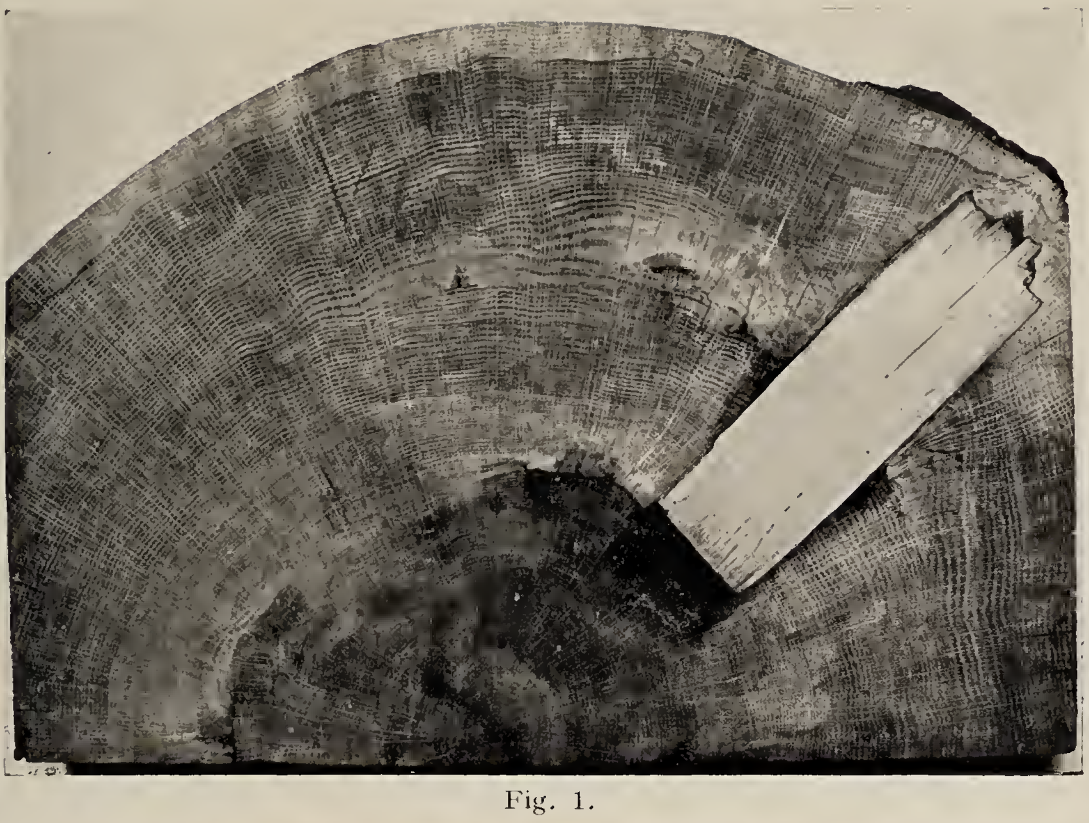


Fig. 1.

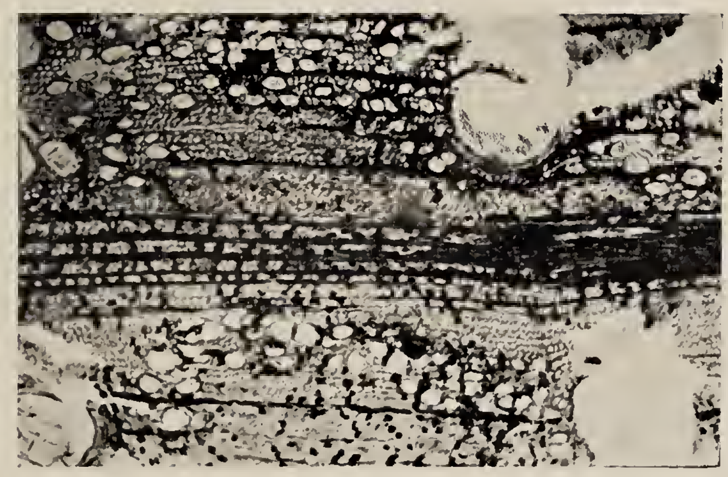


Fig. 2.

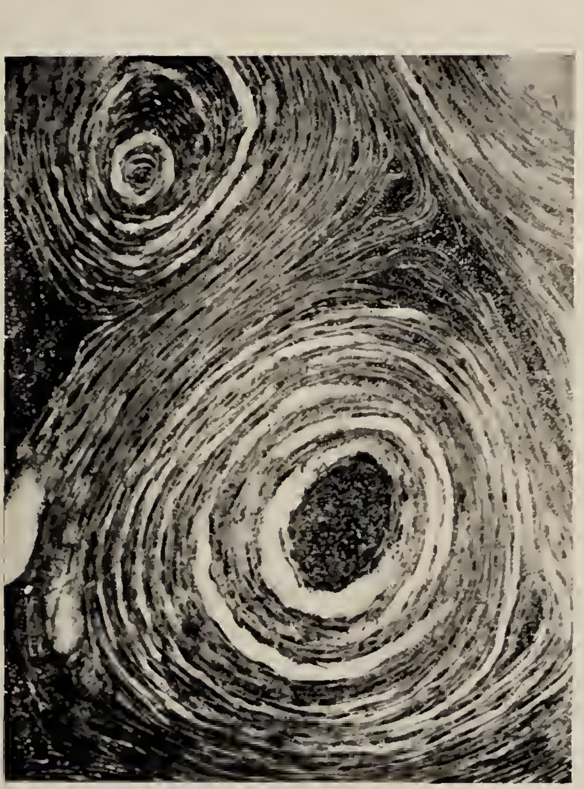


Fig. 3.

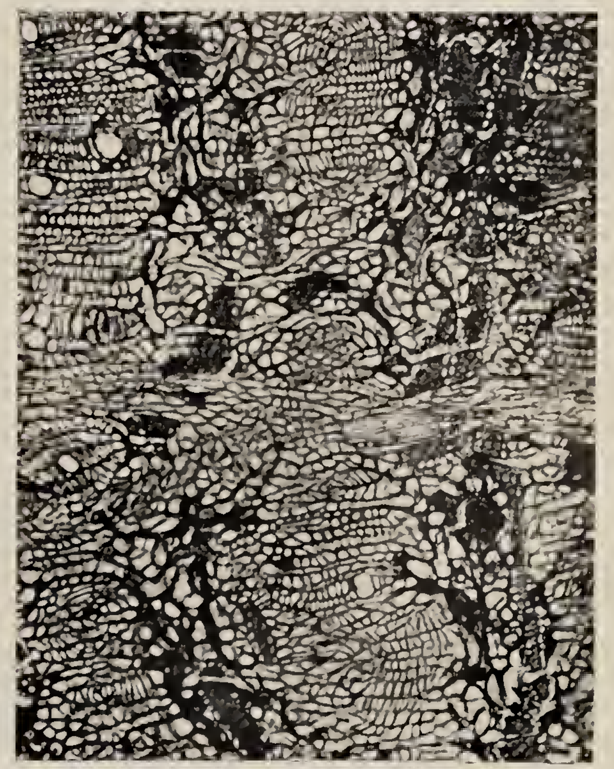
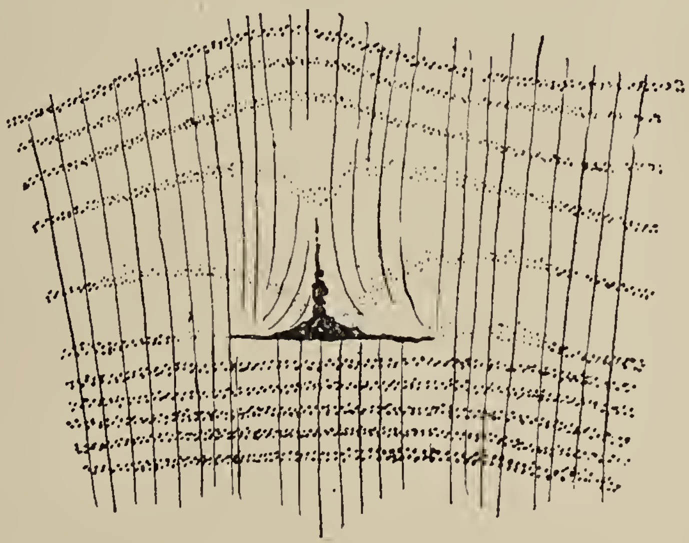


Fig. 4.

DUTHIE.—WOUND HEALING IN A SPECIES OF OAK.

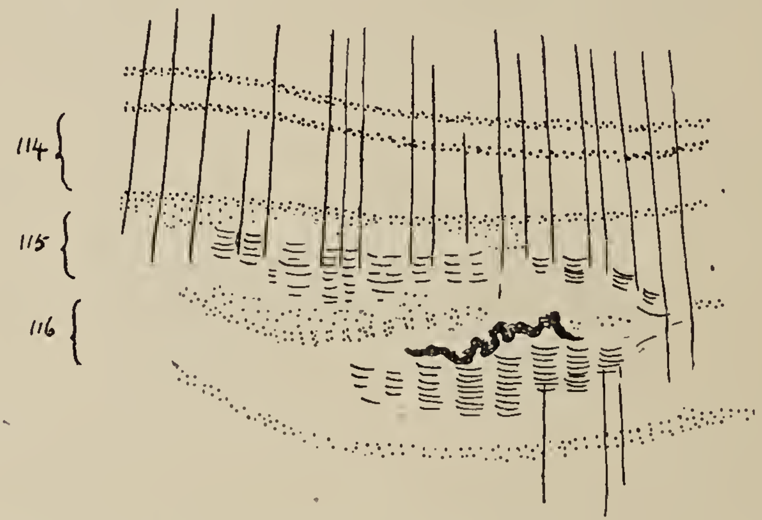
Owing to the reduction of bark-pressure in the region of these injuries, broad callus lips have been produced which have arched over the exposed surface and finally coalesced (Text-fig. 2). As the exposed cambium perished completely there is no cohesion between the callus-tissue and the old wood. In several wounds a thin layer of entrapped cork was found between the callus cushions, and the remains of cortex and bast, which developed on their rounded surfaces before these met and fused, can be seen distinctly. Particularly noticeable are the groups of sclerotic cells which appear as more or less translucent brown specks embedded in masses of thick-walled cells with tanniniferous contents. As healing proceeded the callus lips pressed closely against each other, displacing the outer tissues, until finally the cambium layers came into contact and thickening proceeded normally. Even after the wounds have healed completely the effect of the injury still appears in the broadening of the wood ring immediately following.



Text-fig. 2. Transverse section of part of oak-stem showing wound which has healed completely in two years.

All the wounds considered thus far have exhibited the usual method of healing by the formation of callus cushions from the living tissues at the edges of the wounded area. The remaining injury, which lies about 5 cm. to the right of the peg, has apparently healed in a somewhat different manner (Text-fig. 3).

The broadening of the 114th ring is due to the lateral influence of a rind gall a little to the left, which is not shown in the diagram. The summer wood of each of the two succeeding rings passes into a tissue which at first sight suggests a portion of enclosed phloem. This abnormal tissue appears to the naked eye as a series of undulations each bordered by a darker line. In places the alternation of lighter and darker striations is extremely regular as may be seen to the right of the diagram (Text-fig. 4.) Fig. 4 is a photomicrograph of part of a transverse section cut through this abnormal region. It shows regularly-arranged groups of strongly-thickened fibres which resemble closely those formed in the normal bast and arc in contact with vertical rows of crystal-containing parenchymatous cells. Alternating with these bands of fibre-groups are zones consisting of thick-walled pitted parenchymatous cells often arranged concentrically and intermingled with crushed tanniniferous cells. A few sclerotic nests similar to those found in the normal cortex are also present. A careful examination of transverse and longitudinal sections cut through this region has led to the conclusion that the abnormal tissue has originated in a callus produced by the outgrowth of the living medullary-ray-cells at the surface of the wound: this has in its turn been overgrown by an investing layer produced in the usual way. Apparently the newly-formed layer of normal wood was wounded in much the same manner the following year, and again healed by the development of callus-tissue from the living cells of the medullary rays.



Text-fig. 3. Transverse section of part of oak stem showing callus tissue formed from living cells of medullary rays.

A second slab of oak from the same stem was examined and showed another case of wound healing very similar to the above, but differing from it in that the callus-cushion overarching the abnormal tissue was more distinct.

In this connection it is interesting to notice that Hartig[1] described and figured a case of wound healing in the oak by the formation and fusion of club-shaped swellings from the exposed ends of the medullary rays. The process was, however, not complicated by the additional development of callus-wood from the edges of the wound as in the present instance.

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[1] Hartig. Forstliche Culturpflanzen.

The wound-wood in the vicinity of the rind-galls was also examined in some detail, longitudinal sections as well as transverse being cut where possible. A considerable increase in the amount of wood parenchyma was observed, also the smaller size and more scattered arrangement of the vessels in these regions. The cavities of the vessels were frequently found to be completely blocked with much thickened, lignified tyloses flattened by pressure into polyhedral forms and communicating with one another by means of simple pits. Near several of the wounds these tyloses were packed with starch grains. Thinner-walled tyloses were found to be very abundant in the sap-wood lying to the outside of the embedded peg.

As the tissue of the overarching callus-cushions is much distorted, sections were cut to the right and left of the injuries described above, so as to show the wound-wood in continuity with the normal wood. In several cases the disintegration of a broad ray into a pencil of uniseriate rays was found to occur as the result of the injury, and the gradual compounding of these was noticed. In other cases, however, the rays continued their course undisturbed by the wound-stimulus.

The xylem formed outside the wounded areas after the coalescence of the callus-cushions was also examined. In most cases the wound-wood in these regions showed only non-aggregated small rays. Fig. 2 (Plate II), is a photomicrograph of a transverse section through the wound-wood outside the peg, just where heart- and splint-wood join. Owing to the presence of dark-brown tanniniferous contents in the ray-cells, the compounding process can be seen very distinctly. The *abrupt* formation of broad compound rays was also noticed in the straight grained tissue near several of the injuries, and the same phenomenon was observed in most of the callus-cushions.

During the last two years much has been written regarding the evolution of the different types of medullary rays met with in Dicotyledons and more especially in the Fagales.[1] Eames,[2] from the study of ancestral forms and the development of seedling oaks, has supported the view that the wood of primitive Fagaceæ was entirely devoid of the broad homogeneous "primary rays," which are present together with uniseriate rays in the wood of deciduous oaks. The broad rays are supposed to have arisen phylogenetically by the fusion of uniseriate rays. Bailey[1] has arrived at the same conclusion from an investigation of the traumatic wood of several species of *Quercus*. In the immediate neighbourhood of a severe wound he found only uniseriate rays produced, though a slight injury occasionally caused the abrupt formation of broad rays. Groom[2] has recently reviewed the position and has given it as his opinion that "it is impossible at present to decide whether in *Quercus* the broad-rayed or the narrow-rayed type was primitive." He has also suggested the possibility of the origin of broad rays in *Quercus* and *Alnus* by a fusion of small rays as being merely of physiological significance.

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[1] See "Medullary Rays and the Evolution of the herbaceous habit." New Phyt., Vol. X, p. 362.

[2] Eames, A. J. "On the Origin of the Broad Ray in *Quercus*." Bot. Gaz., 49: 161 166.

The European species *Quercus pedunculata* is not included among the species whose traumatic tissues were examined by Bailey, and it is interesting to notice that its behaviour when wounded is not entirely in accordance with the results obtained by the above investigator, since severe wounding does not invariably cause the production of uniseriate or non-aggregated small rays, but occasionally also the abrupt formation of broad rays.

The writer wishes to express her gratitude to Professor Seward for facilities for working at the Botany School, and for advice in the above investigation.

BOTANY SCHOOL,
CAMBRIDGE. *May, 1912.*

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[1] Bailey, I. V. "Traumatic Oak Woods." Bot. Gaz., 50: 374-380.

[2] Groom, P. "The Evolution of the Annual Ring and Medullary Rays of *Quercus*." Ann. Bot., Vol. XXV, No. C, October, 1911.

DESCRIPTION OF THE PHOTOGRAPHS ON PLATE II, ILLUSTRATING MISS DUTHIE'S PAPER ON WOUND HEALING IN A SPECIES OF OAK.

FIG. 1. Photograph of slab of wounded oak, shewing the the deal peg and the several wounds described in the text.

FIG. 2. Photograph of transverse section of wound-wood outside embedded peg at the junction of heart and sap-wood, shewing the "compounding" of narrow medullary rays.

FIG. 3. Photograph of tangential section of callus-wood outside jagged end of deal peg, shewing changed shape of rays and twisted course of xylem elements.

FIG. 4. Photograph of transverse section of abnormal callus-tissue formed by the fusion of club-shaped outgrowths from exposed medullary ray cells, shewing regularly arranged groups of very thick-walled fibres in bands alternating with thick-walled wood parenchyma often arranged concentrically: also crushed tanniniferous cells (dark).

A DISEASE OF TOMATOES.

By F. T. Brooks, M.A.
(Senior Demonstrator of Botany, Cambridge University),
AND
S. R. Price, B.A.
(Frank Smart Student, Cambridge University).

[With 13 Text-Figs].

IN October, 1911, some diseased tomatoes grown out of doors in the neighbourhood of Bristol were sent to one of us for examination. These fruits bore large diseased areas somewhat depressed below the surface of the healthy parts. On the diseased portions of the fruits three fungi were found, a species of *Cladosporium*, a species of *Macrosporium*, and a fungus having pycnidial fructifications. These fungi were indiscriminately mixed for the most part, but on some of the diseased areas most recently formed only the fungus bearing pycnidia could be seen. It was thought, therefore, that the fungus with pycnidial fructifications might be the actual cause of the rot, the other fungi having appeared later as saprophytes.

In order to determine which organism was the cause of the disease the three fungi were isolated in the usual way by means of plate cultures. Tomato fruits approaching maturity were inoculated with these fungi in the following manner, one kind of fungus only being inserted in each of the fruits:—in opposite sides of each of three fruits two slits were made with a scalpel, and mycelium taken from a pure culture of each fungus was inserted in them, the fruits being placed on glass plates and covered with glass dishes. Three days later a rot had begun around each of the two slits in which the fungus with pycnidial fructifications had been placed, whereas the tomatoes inoculated with *Macrosporium* and *Cladosporium* respectively remained unaffected. After a fortnight the one tomato was completely rotted, whereas the other two were sound. Hence this preliminary trial made it tolerably clear that the fungus bearing pycnidia was the cause of the rot, the *Macrosporium* and *Cladosporium* being of no significance in this case, although it is well-known that species of both of these genera sometimes cause diseases of tomato fruits. Subsequent experiments with the three fungi confirmed the result of the preliminary trial, *viz*,, that the fungus having a pycnidial type of fructification was the cause of the disease.

At a later date one of a consignment of tomato fruits grown under glass in the neighbourhood of Cambridge was found to be affected with the same fungus, the pycnidia, spores, and characters when grown on artificial media being identical with those of the fungus isolated from tomatoes grown out of doors.

IDENTIFICATION OF THE FUNGUS ON TOMATO FRUITS.

As yet few fungi with pycnidial fructifications have been described as causing diseases of tomato fruits. Plowright[1] in a paper on diseases of tomatoes mentions *Phoma destructiva* and *Sphæronema lycopersici* as causing rots of the fruit. The former fungus was associated with a species of *Cladosporium* and a species of *Macrosporium*, both of which Plowright considered to be stages in its life-history; but in the absence of culture and inoculation experiments it is impossible to say whether this was really the case or whether either of these forms was the actual cause of the rot. The characters of *Sphæronema lycopersici* as given by Plowright agree more closely with those of the fungus with which this paper deals and it is possible that they are identical, but Plowright's description of the fungus is too meagre to enable the identity to be established. Massee[2] mentions a pycnidial stage as occurring in the life-history of *Macrosporium solani*, Cooke, which is now considered to be identical with *Macrosporium tomato*, Cooke, the cause of the common black rot disease of tomato fruits, but the characters of the pycnidia do not agree with those of the fungus with which we are now concerned.

Massee has recently described the occurrence on tomato plants in England of the fungus *Diplodina citrullina*, Grossenbacher, or *Ascochyta citrullina*, C. O. Smith, as it is sometimes called, this fungus being the pycnidial stage of *Mycosphærella citrullina*, Grossenbacher. Massee[3] describes this fungus as attacking in an epidemic manner the stems of tomato plants grown under glass. One of us has also had the fungus under observation in Cambridgeshire where it has attacked plots of out-door tomatoes for two seasons in succession. In these cases the lower part of the stem was the region attacked, the cortex being partly destroyed. It occurred to us that the fungus on the tomato fruits might be identical with the *Ascochyta citrullina* mentioned above. The characters of the pycnidia and spores of the fungus on the fruit closely approached those of *Ascochyta citrullina* on the stems of

[1] Plowright, C. B. *The Gardeners' Chronicle*, 1881, p. 620.

[2] Massee, G. *Diseases of Cultivated Plants and Trees*, p. 503.

[3] Massee, G. *Kew Bulletin*, 1909.

tomato plants, and upon sending to Mr. Massee a specimen of the fungus on the fruit, he pronounced it to be "*Ascochyta citrullina*, C. O. Smith, the conidial form of *Mycosphærella citrullina*, Grossenbacher."

The young pycnidia on the tomato were pale brown in colour, and became darker with age, the spores were hyaline and occasionally uniseptate. The measurements both of the pycnidia and spores were about the same as those given by Massee in his description of *Ascochyta citrullina*. When mounted in water and observed under the microscope, mature pycnidia were seen to liberate their spores in a coil-like manner through the ostiole. The pycnidia obtained from the stems of tomato plants liberated their spores in the same manner.

As material of the fungus was available both from fruit and from stem it was thought desirable to grow the fungus from the two sources on artificial media and to perform inoculation experiments. The fungus obtained from the fruit was placed in the stems, and the fungus from the stem was placed in the fruits. In this manner it was hoped to establish more completely the identity of the fungus from the two sources.

CULTURES OF THE FUNGUS ISOLATED FROM THE FRUIT.

On account of the method of liberation of the spores it was easy to obtain them in a fairly clean state and establish pure cultures of the fungus. The spores germinated readily both in water and in a dilute solution of sugar.

On tomato extract containing 10 per cent. of gelatine the fungus grew well, forming a dense white mycelium which began to sink into the medium after 8-10 days, at the same time causing liquefaction of the gelatine. The mycelium did not produce spores when grown on this medium.

On tomato-agar, *i.e.*, agar containing tomato extract, the mycelium grew less vigorously but pycnidia developed in considerable numbers. These fructifications were brownish in colour and similar in structure to those obtained on tomato fruits, but were more variable in size. The spores were similar to those produced by pycnidia that developed in the tissues of the plants. In old cultures the spores exuded from the pycnidia and formed blobs of a pinkish colour at their orifices, though the masses of spores sometimes spread over the surface of the pycnidia or the medium in the immediate vicinity. In these cultures there was often a tendency for the pycnidia to be distributed in concentric circles similar to the manner in which other fungi develop their fructifications on various media, but this tendency was more marked in the case of certain cultures of the fungus originally derived from the stems of tomato plants.

On pure agar the fungus grew much less readily; the mycelium was sparse and only a few pycnidia developed. Fig. 1 represents a microtomed section of one of these pycnidia and Fig. 2 fresh spores from such a pycnidium.

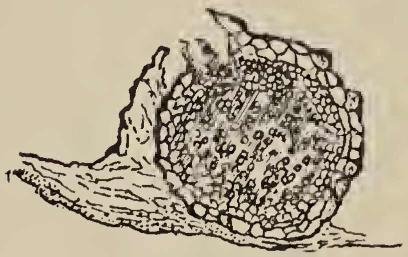

Fig. 1. Fungus isolated from fruit. Section of pycnidium on agar. ×125 diam.

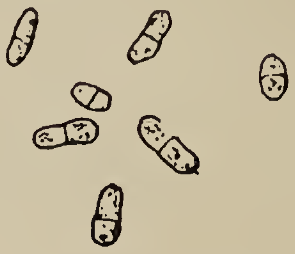

Fig. 2. Fungus isolated from fruit. Fresh spores from pycnidium on agar. ×770 diam.

CULTURES OF THE FUNGUS ISOLATED FROM THE STEM.

Cultures were obtained in the same manner as in the case of the fungus isolated from the fruit. The spores germinated readily both in water and in a dilute solution of sugar.

On tomato-gelatine a dense white mycelium developed which began to sink into the medium in about 8 days and caused liquefaction of the gelatine. No fructifications were formed in cultures on this medium.

On tomato-agar the mycelium grew less vigorously but numerous pycnidia developed. In appearance and structure these fructifications were identical with those which occurred in cultures of the fungus derived from the fruit. The spores, represented in Fig. 3, were similar and in old cultures were aggregated in the same manner at the orifices of the pycnidia. In these cultures also there was a tendency for the fructifications to develop in concentric circles and in one particular series of plates which were kept in a cool position in a North light during December this distribution was well marked, as is shown in Fig. 11, which is a photograph of one of these cultures. Although many other cultures were subsequently kept under approximately the same conditions, the "fairy ring" mode of distribution of the pycnidia was not again so well marked.

On pure agar the mycelial growth was very thin and only a small number of pycnidia were formed. Fig. 4 represents a microtomed section of one of these pycnidia.

The above observations make it clear, therefore, that as regards behaviour on culture media the fungi derived from the fruit and stem respectively are identical.

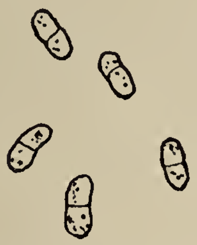

Fig. 3. Fungus isolated from stem. Fresh spores from pycnidium on tomato agar. × 770 diam.

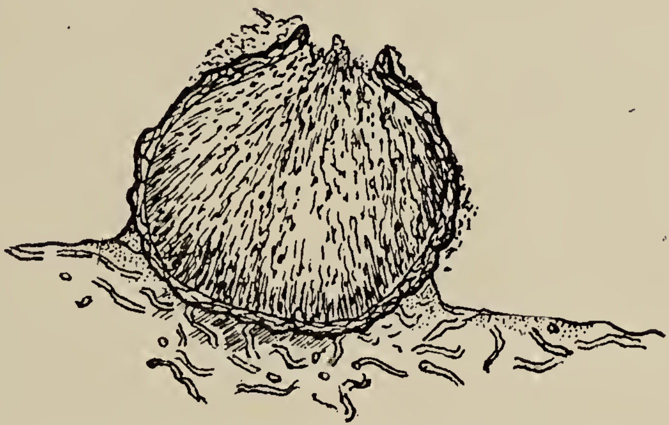

Fig. 4. Fungus isolated from stem. Section of pycnidium on agar. × 770 diam.

INOCULATION EXPERIMENTS WITH FUNGUS DERIVED FROM THE FRUIT.

Experiments showed that with green fruits infection would only result if the fungus, either in the form of mycelium from a pure culture on tomato-gelatine, or of spores, was inserted into wounded parts. In such inoculations a rot began in the immediate neighbourhood of the wound a few days after the fungus was inserted and gradually spread throughout the tissues of the fruit. After 10-14 days numerous pycnidia developed on the surface. Fig. 5 shows a section of one of these pycnidia. The fruits remained

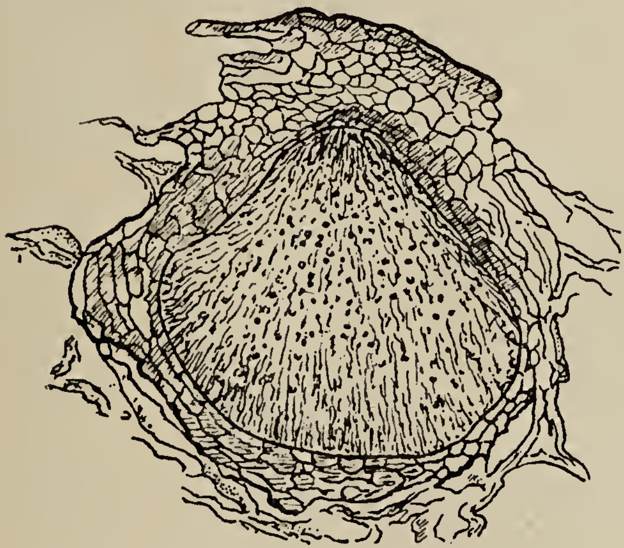

Fig. 5. Fungus isolated from fruit. Section of pycnidium on an inoculated fruit. × 500 diam.

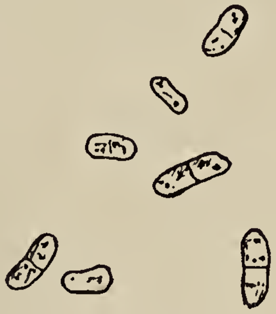

Fig. 6. Fungus isolated from fruit. Fresh spores from pycnidium on an inoculated stem. × 770 diam.

sound in control experiments. With ripe fruits, however, experiment showed that infection sometimes resulted when the mycelium was placed on uninjured parts.

Inoculations of wounded parts of stems of tomato plants were also made with the same mycelium. For this purpose a longitudinal slit was made in the stem about an inch above soil level and some mycelium was inserted, after which the wound was covered with tinfoil. All inoculations were performed as far as possible under sterile conditions. Other plants were kept as controls. The foliage of nearly every plant thus inoculated began to wilt about 7-8 days after the fungus was inserted. Fig. 12 shows one of the wilted plants and one of the control plants side by side. The affected plants subsequently died and in some of them pycnidia of the same character as those previously described, developed in the neighbourhood of the wound. Fig. 6 shows spores obtained from one of these pycnidia. In connection with these inoculations it was noticed that pycnidia were not formed so abundantly as in inoculation experiments made with the fungus originally derived from tomato stems. To make the story complete the fungus was plated out from these pycnidia and in cultures it proved to be identical with the fungus which had been used for inoculation. Upon examination of the tissues of plants which were successfully infected the

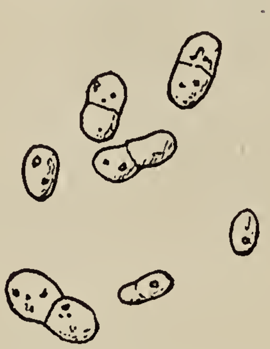

Fig. 7. Fungus isolated from stem. Fresh spores from pycnidium on an inoculated stem. × 770 diam.

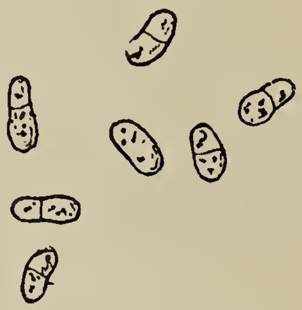

Fig. 8. Fungus isolated from stem. Fresh spores from pycnidium on stem infected in nature. × 770 diam.

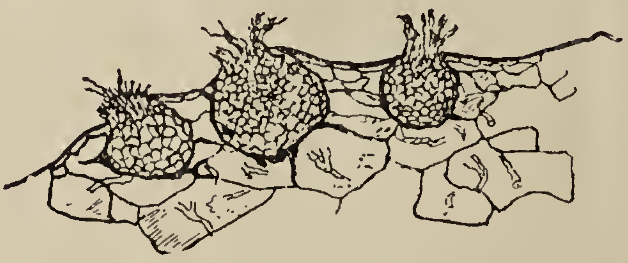

Fig. 9. Fungus isolated from stem. Section of young pycnidia on an inoculated fruit. × 125 diam.

mycelium was found to have extended upwards and downwards both in the vessels and in the cortex. In the few plants which did not become infected after of inoculation, the mycelium had evidently failed to develop.

INOCULATION EXPERIMENTS WITH FUNGUS DERIVED FROM THE STEM.

In almost every case when some of the mycelium grown on tomato-gelatine was inserted in a wound made in the stem of a healthy tomato plant, infection resulted and pycnidia of the same

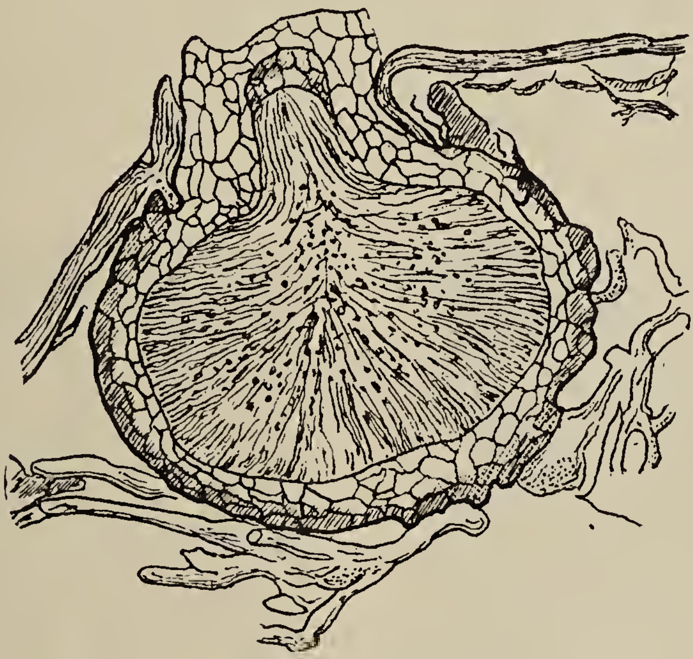

Fig. 10. Fungus isolated from stem. Section of older pycnidium on an inoculated fruit. ×500 diam.

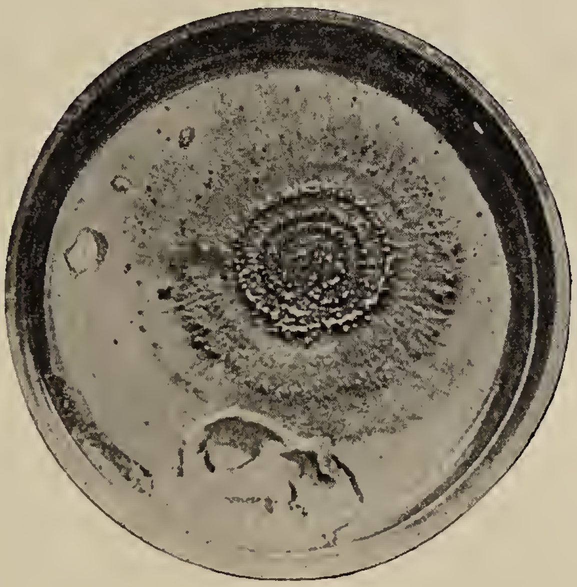

Fig. 11. Fungus isolated from stem. Photograph of culture on tomato-agar.

character as those previously described were formed in the tissues. Fig. 13 shows the wilting of a plant inoculated with this mycelium side by side with a control plant. The fungus plated out from these pycnidia agreed in cultural characters with the fungus which had been used for inoculation. Fig. 7 represents fresh spores obtained from these pycnidia. Fig. 8 shows fresh spores obtained from a plant infected in nature.

The same mycelium placed in wounded parts of the fruits caused rotting of the tissues and formation of pycnidia as previously described. The fungus plated out from these pycnidia was identical with that used for inoculation. Figs. 9 and 10 represent sections of these pycnidia in different stages of development.

The results of these inoculation experiments make it clear that the fungus causing a rot of the fruit is identical with that which induces canker on the stem.

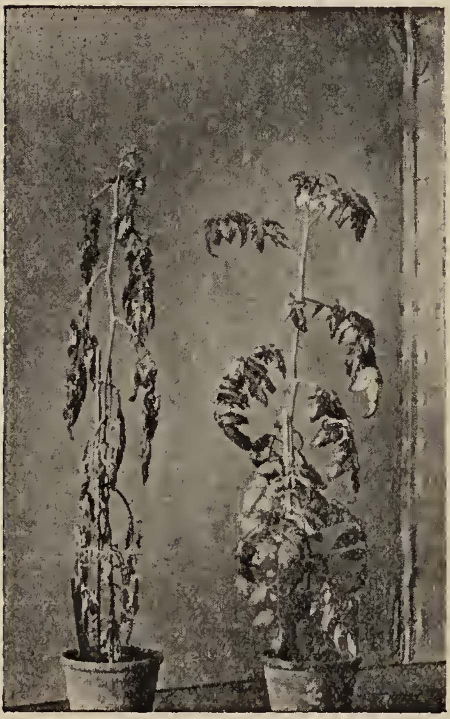

Fig. 12. Photograph of plant inoculated with the mycelium of the fungus isolated from the fruit. A control plant is at the side.

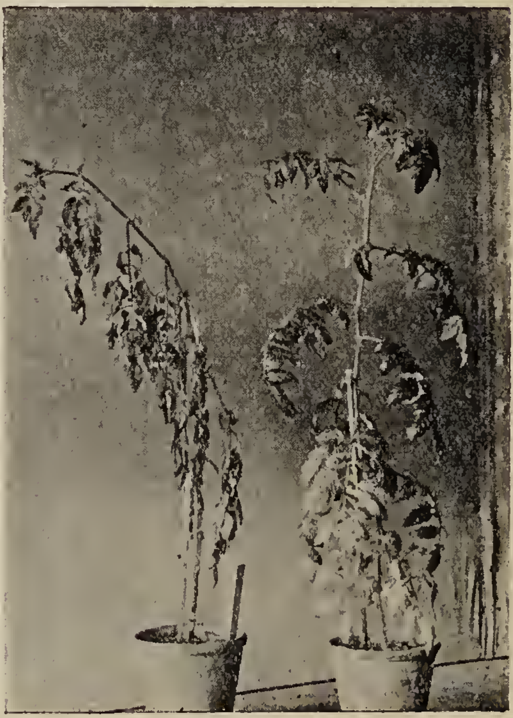

Fig. 13. Photograph of plant inoculated with the mycelium of the fungus isolated from the stem. A control plant is at the side.

The Ascus Fructifications of the Fungus.

Grossenbacher[1] has shown in America that *Diplodina citrullina* (C. O. Sm.) Grossenbacher, or *Ascochyta citrullina*, C. O. Smith, as it has also been called, is the pycnidial stage of the Ascomycete,

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[1] Grossenbacher, J. G., in N.Y. Agric. Expt. Sta., Geneva, N.Y., Technical Bull. No. 9 (1909).

Mycosphærella citrullina, Grossenbacher. This fungus causes a serious disease of melons in the United States, the pycnidial stage there being followed by the formation of perithecia which, however, do not develop until the tissues are dead or dying. We cannot find any record of the perithecial stage having been found in this country, and in the course of our own work perithecia were not seen, although plants and fruits killed by the fungus were kept in an exposed situation during the winter in order to try to induce their formation.

GENERAL REMARKS.

As with so many other pathogenic fungi little is yet known of the manner in which infection by this fungus occurs in nature. The facilities which might enable such a matter to be solved have not been available to us. Such problems can be best studied in tomato houses and gardens developed on practical lines, although used primarily for experimental purposes. At present we do not know of any place in England where such work can be pursued in an adequate manner.

In one plot of out-door tomato plants in Cambridgeshire the disease occurred two years in succession, and in view of the apparent absence of a perithecial stage in this country and of the fact that the tomato plant is an annual, it is not clear how the disease is propagated from one year to another. It is possible that the mycelium hibernates in the dead tissues of affected plants, and it may be that portions of diseased plants left on the ground instead of being burnt are the means of reinfection if plants are set out on the same plot the following year. There is no evidence yet that the fungus is propagated in the seed. On out-door plants the disease does not appear to develop until almost fully grown. In the plots referred to above only 3 per cent. of the plants were affected and the distribution of diseased plants was sporadic, so that the disease is not likely to become a serious pest to growers of out-door tomatoes. In the case of tomatoes grown under glass, Massee[1] has already pointed out how severe an epidemic this fungus may cause on account of the conditions of growth being so favourable for its development. In consequence of its virulence under these conditions it is included in the list of pests scheduled by the Board of Agriculture, under the Destructive Insects and Pests Acts.

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[1] Massee, G. *Kew Bulletin*, 1909.

NUCLEAR OSMOSIS AND MEIOSIS.

By J. Bretland Farmer.

A THIRD instalment of Professor Lawson's nuclear studies has just appeared in the Transactions of the Royal Society of Edinburgh. In it the author develops further some of the views put forward in his previous memoirs, and makes certain observations in reply to a brief criticism upon them which I contributed a few months ago to this journal (Vol. XI, p. 139, 1912).

I may say at the outset that I observe with great pleasure that Professor Lawson agrees with the results, as regards the essential facts of meiosis, which have been arrived at in my laboratory during the last few years. Differences in detail of course there are, but a near examination lessens their importance and I shall refer to this aspect of the matter later on. It is necessary, however, to enter a little further into his hypothesis of "nuclear osmosis," inasmuch as some of the remarks made in the review referred to above appear to have been misunderstood, and so far as I have been able to discover, none of the criticisms have been met.

I gladly take this opportunity of putting right one point in my previous communication. In discussing Dr. Lawson's statement that no contraction of the chromatic mass occurs during the stage often described as Synapsis, I referred to his own figures, and pointed out that they as a matter of fact did show a very considerable contraction of the chromatic tangle. Unfortunately, however, I included amongst them his Fig. 13, which in the text he had exempted from use in this connection, by saying that it did not represent a median section. In the sentence immediately following it is stated that "All of the other figures [*i.e.*, except 13] were drawn from sections that were cut in a median plane—or nearly so—through the chromatin mass." On turning to the explanation of the figures, however, I find it said of Fig. 13 "The same. The nuclear cavity enlarged still more." And of Fig. 14, "The same, from a section that has not been cut in a median plane throug hthe chromatin mass." There is obviously discrepancy and confusion here, and although I sincerely regret the error which has arisen therefrom, I cannot hold myself to be solely responsible for the mistake.

However, the matter is of no great consequence, for in the Figs. 1—12, about which there is no contention, a contraction of about 25% as compared with Fig. 1 is shown. Any one can easily verify this for himself. It is therefore hardly possible to accept Professor Lawson's statement that "The original paragraph itself is a complete reply to the criticism." I do not think the matter of the diminution in the space occupied by the chromatin is of "secondary importance" as Professor Lawson now suggests. When an author is very confidently indulging in speculation, one may fairly require that facts at any rate should be treated with respect. What may appear to be of "secondary importance" to-day may assume a very different aspect in the light of more complete knowledge, and it is of infinitely greater value, in the long run, to get at the facts than to spin hypotheses, be they never so attractive.

Professor Lawson appears to think I have misrepresented him in my remark as to his use of the term permeable membrane in connection with the alleged osmotic process. He says "The term I have *continually* used throughout the paper is a *permeable plasmatic membrane*" (the italics are his own). In the first place, on turning to the paper itself (Nuclear osmosis, p. 144) I find the following statement:—

> "Everything necessary to promote osmotic diffusion is present, there is a permeable membrane and substances of different chemical composition and presumably of different density on either side of it. It is therefore not difficult to understand the gradual diminution of the karyolymph, as shown in these figures, on the basis of osmotic diffusion. The karyolymph has passed out into the cytoplasm by exosmosis."

Will Professor Lawson, in the face of this quotation, still maintain that I have misrepresented him?

In the second place, even if we waive the question as to the exact nature of the nuclear membrane, and agree to call it a plasmatic one, this is still not *ad rem* in so far as an osmotic process is concerned. It is not with the plasmatic character, but with the osmotic property of the membrane that we have to do. A *permeable* plasmatic membrane would be about as effective in the matter as a permeable or perforated bladder. *Semi-permeability* (or selective permeability) is, of course, one of the essential conditions in the absence of which no osmotic pressure could be either set up or maintained. Is it possible that Professor Lawson himself is not clear as to the difference between osmotic and ordinary diffusion processes? If so his description of chromatin as "an osmotically active substance" at a time when it "is undergoing a change to a more condensed form" (Study in chromosome reduction, p. 604) becomes explicable though it still remains unintelligible.

If, however, Professor Lawson means by exosmosis or "osmotic diffusion" of the karyolymph a mere diffusion of nuclear sap from the nucleus into the cytoplasm, consequent on the abolition of the semi-permeable character of the plasmatic nuclear membrane which was hitherto responsible for the maintenance of nuclear turgor, then any contraction of the latter will depend solely on the surface tension properties of this nuclear membrane. The whole achromatic spindle, supposed to arise through the distortion of the cytoplasmic reticulum which is assumed to be coherent with the membrane, must then be attributed to the effects of surface tension alone. But this aspect of the problem seems to have escaped him altogether, or at any rate it has not been discussed. And in the absence of evidence to the contrary we may be permitted to doubt whether the surface tension of the nuclear membrane under the prevailing conditions would be competent either to produce or to effect such a distribution of strain as would account, in any way whatever, for the origin and peculiar characters of the achromatic spindle.

But Professor Lawson appears to desire to have his cake and eat it—*i.e.*, to postulate a membrane endowed with qualities enabling it to permit of loss through diffusion outwards (exosmosis) while at the same time it is maintaining an osmotic pressure within; for he speaks of the chromatin as an "osmotically active substance" as effective at a time when, on his own showing, karyolymph is passing out of the nucleus.

I am further charged with having, in my review, passed over "The discovery of the stages showing the persistence of the nuclear membrane throughout the prophase" (*loc. cit.*, p. 617). I am not quite clear wherein the discovery consists. If the alleged closing in of the membrane over the chromosomes and its partition over their several individual surfaces is meant, I would remark that I did refer to this, and with a scepticism which Dr. Lawson's reply has done nothing to allay. If, however, something else is intended I would point out that it has long been known that the nuclear membrane may persist throughout the prophase and even on to the metaphase of mitosis. Such an example is afforded by *Fucus*, which I think would be a difficult case in many respects to reconcile with Professor Lawson's hypothesis; and there are others besides.

It is also alleged that I omitted to mention "Three important phases of mitosis" of which it is suggested that the hypothesis of nuclear osmosis offers "A fair and rational explanation." (i) the origin and formation of the achromatic fibrils, (ii) the attachment of the fibrils to the chromosomes, (iii) the movements associated with the resolution of the multipolar figures into a bipolar arrangement (*loc. cit.*, pp. 616—617). I am at a loss to understand this, because as regards (i) and (ii) I expressly pointed out what appeared to me to be some of the obstacles in the way of accepting the proposed explanation. It seemed to me, and seems so still, that the "explanation" introduces new difficulties without explaining any of the old ones. I may add that the suggested mode of transition from the multipolar to the bipolar position indicated by Dr. Lawson appears to invoke purely gratuitous assumptions as to properties and behaviour of a reticulum under the postulated conditions of strain. I regret that Professor Lawson should apparently have overlooked my remarks on the aforesaid matters, for he is apparently quite unaware of the number of points in which his hypothesis bristles with difficulties. It is of little use to speak of "convincing proofs," "irresistible conclusions" or even of "belief" to those who feel, as I do, that the arguments are fallacious and the conclusions are unsound.

The treatment accorded to the origin and behaviour of the interzonal spindle (*i.e.*, between the two daughter-nuclei during the anaphase) is another example of the way in which awkward points are shelved. The whole development, contour, extension towards the peripheral cell-wall, and especially the appearance and position of the cell-plate, should have all been considered in connection with any comprehensive theory of the mechanics of mitosis. It is not enough to invoke hypothetical relaxation of the fibres, nor to be assured that there "is no doubt" in the author's mind that:—

> "These threads represent the same state of tension expressed in the achromatic figure of the later prophase and metaphase. The lines of tension have merely shifted with the movements of the chromosomes."

A passage of this sort suggests a lack of appreciation of the fundamental distinction between a mere expression of opinion and a scientific reasoned argument.

A series of facts, with which the author has not as yet dealt, appears to me to be specially difficult to reconcile with the hypothesis that nuclear osmosis constitutes a fact of serious importance in mitosis. It is well known that the whole spindle, in certain cells, may be *intra-nuclear*, and this from the time of its first appearance; and yet the structures themselves so precisely resemble the extra-nuclear spindles in every other respect, that it is impossible to regard them as fundamentally distinct in character. Intra-nuclear spindles have been recognised in a number of animal cells, and the example of *Fucus*, already quoted, is only a little less striking. In the latter plant the spindle is partly extra-nuclear, *i.e.*, cytoplasmic, and partly intra-nuclear, and indeed the nuclear wall persists as a barrel-like body enclosing the spindle and chromosomes even during the metaphase. There is no need to regard the spindle fibres as "pushing into" the nucleus. They appear to originate by differentiation from the nuclear contents, just as the fibrils in the cytoplasm arise, by differentiation, from the cytoplasmic substance. And in both positions they seem to map out lines of force or of strain.

Amongst the numerous points which will have to be worked out in detail in connection with any theory which aspires to explain the mechanics of mitosis will be:—(i) the shape of the spindle, its straight and its convex appearance in profile; (ii) the lack of adherence to the cytoplasmic boundary, so frequently observed, *i.e.*, its differentiation and blind ending in the cytoplasm; (iii) the details of the convergence of multipolar to bipolar arrangements, and the analysis of the causes of these rearrangements; (iv) the definite arrangement of the equatorial plate, and the polarised character of the spindle in the connection therewith; (v) the frequent suppression of the peripherally directed fibres, present in so many cells, during this period of metaphase; (vi) the detailed analysis of the processes leading to the formation of the interzonal spindle—a study of those forms of belated cell-wall formation, *e.g.*, those encountered in some endosperms, might well help to elucidate this; (vii) the intra-nuclear spindle.

Although these suggestions are by no means exhaustive, they may, I think, be taken as representing a fair sample of the problems that have to be faced. It is by no means likely that their entire solution will be achieved in the immediate future, nor indeed until we obtain to a far deeper and more accurate knowledge of the microphysics of the cell, and of the modifications of structure and consistency depending on chemical and physical change, than we possess just now. For the present, then, we must continue to work with hypotheses. But we may reasonably ask that, while embracing the observed facts, these hypotheses should not conflict with the principles of elementary physical science.

We may now leave these matters and turn to the main results of Professor Lawson's most recent communication. Here we reach ground where, happily, a closer agreement is possible. The plant principally selected for the investigation of the meiotic phase was a species of *Smilacina*, and it has evidently turned out to be a most fortunate choice. Some of the stages which have proved troublesome in forms otherwise satisfactory, seem to exhibit a clearness that leaves nothing to be desired. The chief results are, briefly, a follows:—The chromatic substance, as it differentiates from the resting nucleus at the prophase of the first meiotic division is seen to be double from the first. In this respect Professor Lawson's observations are in precise accord with our own (Farmer and Digby, On the Somatic and Heterotype Mitoses in *Galtonia candicans*, Brit. Ass. Rep., Sheffield, 1910). That is to say, each chromosome arises with a structural arrangement *already in existence* identical with that which finds its expression in the longitudinal fission during the ordinary somatic mitosis. It is this duplex character which has been interpreted by Grégoire and his pupils to represent the lateral approximation of pairs of somatic chromosomes to form the heterotype bivalents, owing to the failure to recognise it at these earlier stages. It appears clear, however, that the explanation advanced by Grégoire cannot be fitted to the case of *Smilacina*, any more than it could to *Galtonia*. Each duplicate filament of *Smilacina*, represents one longitudinally split somatic chromosome, *for they are present in the full pre-meiotic or diploid (2x) number.* There appears to be no room for mistake, inasmuch as they are described and figured as entirely separate from one another, furthermore they are apparently free from lateral or other anastomoses which in *Galtonia* and other plants so often serve to mask or obscure the real course of events. Later on, at a stage corresponding with the "second contraction" of some authors, the split pre-meiotic chromosomes join in pairs, conjugating laterally to form the heterotype bivalent (x) chromosomes. The longitudinal fission in each (pre-meiotic) chromosome persists more or less obviously until the metaphase of the next (homotype) mitosis, when it becomes finally effective and brings about the separation of the daughter chromosomes at this stage.

There is, of course, nothing very new in all this, but it furnishes a welcome and important confirmation of that interpretation placed on the critical stages of meiosis which is becoming more widely adopted at the present time.

It is about ten years ago since several investigators, ourselves among the number, working independently of each other, put forward these views. They were set forth in some detail in a paper published in 1905 (Farmer and Moore) to which Professor Lawson makes frequent reference. With the increase of knowledge, amplification and corrections in detail have naturally been made, but the main results then reached have been, in essentials, confirmed by further research on the part of my co-workers and myself, as well as by others. Different material varies greatly, both as regards the clearness with the process can be followed, and the certainty with which the evidence can be sifted, and it is to this circumstance that the divergence of views which still exists is to be largely attributed. In this connection the investigations on hybrid and mutating plants have proved of especial value. Thus Gates has observed important stages in his studies on *Œnothera* (subsequently confirmed by other students of the cytology of this genus) which appear to be irreconcilable with the very different explanation first advanced by Grégoire and his pupils.

It is unnecessary for me to enter at greater length into the controversy which has been going on for a number of years concerning the time at which meiotic pairing of the chromosomes to form the bivalents occurs. Nor is it necessary to discuss the radically different interpretations which have been placed on the parallel threads that can be observed during the early stages of prophase as I have already given a brief epitome of them in a recent note on "Telosynapsis and Parasynapsis" in the current volume of the Annals of Botany.

Professor Lawson, in quoting the work which has issued from this laboratory, curiously enough rather exaggerates points of difference between us, but it seems a pity that in doing so he should have imputed to us opinions which are the very reverse of those which we have advanced. I do not propose to enter at full length into this matter, for controversy on matters of history where the evidence is readily accessible is useful only in so far as it serves to prevent error from becoming stereotyped, as it is apt to do if allowed to go entirely unchallenged.

Professor Lawson states on p. 605 :—

> "But this diminution [in the chromatin volume], which is a very slight one, I do not interpret in any sense as a 'synaptic contraction' as generally understood by many writers (Farmer, 1905; Grégoire, 1910; Overton, 1909; Digby, 1910, and others, and others), nor do I believe it to be a feature peculiar to meiosis."

Now this is thoroughly misleading, for while Grégoire and his followers have regarded the conjugation of the somatic chromosomes as the essential features of this stage, my co-workers and I have simply regarded it as a puzzling feature which we were bound to accept, though we could not explain it. But we have held that what Grégoire believes to indicate lateral approximation of somatic (or premeiotic) chromosomes in reality represents the *longitudinal fission of the spireme*, precisely as Professor Lawson appears to do. And confirmatory evidence of this has been advanced both by Dr. Fraser and by ourselves in several papers published during the last two years.

There are other passages in which Professor Lawson betrays a singular lack of critical historical feeling; I will only quote one example :—

> "It should be remembered that the interpretations of Farmer (1905) .... are based on the assumption that the chromatin consists 'of one continuous spireme, which segments transversely so as to form definitive chromosomes.'"

Such a statement is not in accordance with fact, it does not fairly describe our position in 1905, and still less does it represent the views we have advanced in more recent papers. It is quite true that we frequently spoke of a continuous thread, for in 1905 the opinion was almost universally held that the spireme did consist of an unbroken thread, which only later segmented and formed the chromosomes. But we ourselves ventured to throw doubt on the view, and described examples in which there was definite proof either that a continuous spireme was never formed (*Blatta*), or that at any rate that it was not present in the early stages (*Tradescantia*), "It is quite certain that during these early stages of prophase there is no continuous spireme present. The ends of the stainable threads can be clearly recognised." (Farmer and Shove, Q.J.M.S., 1905, p. 653). Furthermore, in discussing the question as to whether or not there is a continuous spireme in *Lilium*, though it was believed that such was formed later on (and as I now think erroneously), it is remarked, "perhaps the matter is not of very great importance." .... (Farmer and Moore, 1905, *loc. cit.*, p. 508).

The belief in a continuous spireme, so prevalent at that time, was, as a matter of fact, one of the serious theoretical difficulties we had to encounter in arguing for the persistence of chromosomes from one cell generation to another, and we devoted considerable space to the attempt to show that the commonly entertained belief was not really well founded (*loc. cit.*, pp. 543-5). And with the advance of knowledge we, with others, have accepted the possibly morphological, as well as the physiological, individuality of the chromosomes in the spireme, as well as during other phases in the life history of the nucleus.

The principal credit for the recognition of this independence of the chromosomes during the spireme stage of prophase belongs unquestionably to Grégoire and his pupils. Nor does any difference of interpretation of the events of "synapsis" seriously touch this claim, though it does somewhat affect the supposed evidence on which the generalisation itself was based.

Professor Lawson draws attention to the well nourished condition of the spore mother-cells, and he appears to see in this accumulation of available nutrative material an explanation of the rapid succession of the two meiotic divisions. Discussion of the points raised by this or kindred suggestions would be out of place at the present time, inasmuch as a further paper is promised wherein the author expects to deal more fully with this important question.

Imperial College of Science
and Technology, *December 2nd, 1912.*

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

I—Introduction.

TWENTY years ago Klebs (67)[1] published the first comprehensive work on the Flagellata in which these organisms—usually treated by zoological writers as a division of the Protozoa—were studied in detail from the botanical as well as the zoological point of view. Klebs pointed out that the Flagellata are a heterogenous assemblage in which, more than in any other Protista, the former distinctions hitherto drawn between the animal and vegetable kingdoms entirely vanish; that the Flagellata may be regarded as a central group from which the various classes of Protozoa have arisen; and that this group also embraces a number of specialised lines of descent—including several distinct lines leading to the lower Algæ. The results of recent work, some of which it is proposed to summarise and discuss here, have in the main confirmed the views expressed by Klebs in his diagrammatic scheme of the phylogenetic relationships between Flagellata and Algæ—with certain modifications arising from the discovery of new forms and the reinvestigation of forms whose structure and development had been imperfectly known—and have lead to great advances in our knowledge of the phylogeny of the Algæ, and to striking changes in the classification of the Green Algæ in particular.

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[1] References to Literature will be given in a Bibliography at the end of the concluding portion of this article.

It is now generally recognised that a division of the Flagellata into forms referable to the vegetable kingdom (forms bearing chlorophyll, having a cell-wall of cellulose, and having no mouth or other means for ingesting solid food) and forms referable to the animal kingdom (forms without chlorophyll, without a cell-wall or with a wall not consisting of cellulose, and having a mouth or other means for solid ingestion) would be absolutely unnatural and could only be made by ignoring genetic relationships which are perfectly obvious. Moreover, such a division would leave out of account a large number of organisms which could not logically be placed in either division. A better criterion would seem to be afforded by the consideration that in the lowest organisms regarded as animals, somatic growth and reproduction by fission are marked by active mobility, the flagellate cells growing and dividing in this condition; whereas in the lowest organisms regarded as plants, somatic growth and division are marked by stability, and the flagellate cells do not grow and divide but may conjugate and give rise to a sedentary zygote. We shall see, however, that even this criterion—which has led to the inclusion by zoological writers of the greater part or even the whole of the Flagellata in the animal kingdom as a class of the Protozoa—is vitiated by the occurrence of transitional forms through which certain Flagellate groups shade off almost imperceptibly into definitely Algal organisms.

Assuming that the lower Algæ have arisen from a Flagellate ancestry, the work of the majority of recent writers on the phylogeny of the Algæ has been directed towards the tracing of the lines of descent leading from certain Flagellate groups to the lower Algæ, and to the formulation of a system of classification which shall reflect the phylogenetic relationships thus disclosed. Of the four main groups into which the Algæ have usually been divided, the Blue-green Algæ are probably related in some way to the Bacteria, but the origin and affinities of both divisions of "Schizophyta" are quite uncertain, though they are possibly of Flagellate origin; the Green Algæ may be traced, through transitional forms, to at least two distinct sources among the green Flagellata; the Brown Algæ have similarly been shown, especially by quite recent work, to have arisen from certain Flagellata with brown chromatophores; while as regards the Red Algæ there appears at present to be no better-founded view than that suggested by Klebs—that they may have arisen from Brown Algæ.

In recent speculations concerning the evolution of plants it has generally been assumed that the earliest vegetable organisms possessed chlorophyll and were autotrophic (photosynthetic) forms, their immediate ancestors being autotrophic Flagellates;

that the Green, the Brown, perhaps also the Red, and more doubtfully the Blue-green Algæ arose respectively from similarly coloured Flagellata; and that the various groups of Fungi have arisen independently from different Algal forms—though some fungal series may have come directly from Flagellata. However, Vuillemin (144) has pointed out that in our ignorance concerning the conditions under which the earliest forms of life appeared, we are hardly justified in assuming that photosynthetic organisms necessarily preceded heterotrophic organisms in time, and that from this point of view the nitrogen-fixing Bacteria have as good a claim as chlorophyll-bearing organisms to be regarded as the nearest living representatives of the earliest forms of life. We cannot, however, construct a series of existing forms connecting the Bacteria with the main autotrophic Algal phyla, though it has been suggested (Doflein, 40; Zuelzer, 158) that the Bacteria may have given rise, through the Spirochætes, to the Flagellata.

Starting from simple coloured autotrophic organisms, Brunnthaler (6) argues that the Red Algæ are the most ancient group of plants, on the grounds that (i) the earliest plants were in all probability free-swimming Flagellate forms, and no such forms occur among the present-day Red Algæ; (ii) the red pigment of the Rhodophyceæ is an adaptation to life in the deeper waters of the sea and in the dim light of the primitive world with its dense cloud canopy, since this pigment absorbs the rays in which that light would be rich; (iii) the present-day Red Algæ show hardly any primitive types, and motile free-swimming reproductive cells are absent from the group. The Brown Algæ would come next; that this is a younger group is indicated by the great diversity in structure of the reproductive organs, the constant presence of flagellate reproductive cells, and the adaptation of the brown pigment to the absorption of light more closely approaching in quality that of the bright sunlight reaching the surface of the present world, but still with an atmosphere richer in water vapour than that of to-day. Meanwhile, the primitive Red Algæ had become adapted to the dim ancient light, and therefore restricted to the deeper sea, leaving the upper waters as an open field for the evolution of the new brown seaweed population. The Green Algæ, finally, are the youngest group to appear in the succession outlined by Brunnthaler, their green colour being an adaptation to the fuller light (richer in the less refrangible rays of the spectrum) of modern times; the early forms were marine, but after possessing the upper waters of the sea and invading estuaries they became adapted also for life inland in fresh water. According to Brunnthaler, there is no direct relationship between the present-day Algæ and Flagellata, though the earlier Flagellates may have given rise to the Red Algæ; the living Flagellata he regards as the termination of an ancient series of organisms which have evolved independently of the Algæ.

II—GENERAL CHARACTERS OF THE FLAGELLATA.

Without dealing further with such questions as these, it may be noted in passing that there is a good deal to be said against the assumption, which has frequently been made, that the Flagellata represent the most primitive of known organisms; this claim may perhaps quite as reasonably be put forward for bacterial forms or for the simpler amœboid types of Protozoa. For instance, there are grounds for regarding a flagellum as a specialised type of pseudopodium, since between the blunt pseudopodium of an *Amœba* and the vibratile flagellum of a typical Flagellate, there are various intermediate forms of protoplasmic outgrowth concerned in locomotion or ingestion of food or other functions. In any case, however, the Flagellata appear to include forms leading by a series of transitional types to the lower Green and Brown Algæ, and these are our chief concern here.

The characters given by Klebs as distinguishing the Flagellata from the motile unicellular Green Algæ—the Chlamydomonads, which are still included by zoological writers in the Flagellata under the name "Phytoflagellata"—may be enumerated as follows. Body unicellular or a colony of cells, cell uninucleate with a thick or thin external layer of protoplasm—the *periplast*—in which *amœboid changes of form* may take place. Outside this a non-living investment of the cell is frequently present, of varied form and often not closely adherent to the body. Specialised anterior end of clear protoplasm bearing one or more flagella. Organism always remaining capable of movement. Nutrition either *holozoic* (solid food being taken by pseudopodia, through a specialised mouth, or otherwise), *saprophytic or holophytic.* In the last case the chromatophores are green or yellow-brown, and may take the form of bands, plates or discs. *True pyrenoids entirely absent.* Paramylum, leucosin, or a fatty oil the visible anabolites (products of assimilation). *Starch entirely absent. Reproduction by simple longitudinal fission*, usually beginning at the anterior end of the body. Individual always capable of forming resting cysts. *Gamogenesis apparently entirely absent.*

It may be noted that recent work has made it extremely difficult to frame a definition of the Flagellata which shall separate this group sharply from the Protozoa on one hand and the lower Algæ on the other. Exceptions have to be admitted in connexion with almost every character hitherto given in definitions of the group. The body usually has a definite anterior end from which one or more flagella arise, but in *Multicilia* the numerous flagella spring from various points of the spherical body; the flagella are usually motile and unbranched organs, but in certain Chrysomonads they are non-motile and even branched, corresponding with the pseudopodia of various Protozoa; the visible product of anabolism is usually either oil or leucosin or paramylum, but starch is formed in certain Chrysomonadineæ (e.g., *Cryptomonas*) and in the Polyblepharidaceæ (if these be regarded as Flagellates rather than Chlamydomonadine Algæ); the great majority are uninucleate, but the Trypanosomes have two nuclei, while *Multicilia lacustris* is described as having a large number; as a rule, division is longitudinal and occurs in the motile phase, but it is sometimes transverse (e.g., *Oxyrrhis, Stylochrysalis*) and it may occur exclusively in a resting state; sexual reproduction is usually absent, but a sexual process has been shown to occur in various genera belonging to different groups of Flagellata (39, 50, 118, 121).

In Senn's account (135), which was published in 1900, the Flagellata fall into seven divisions. Three of these comprise only colourless heterotrophic forms (with holozoic, saprophytic, or parasitic nutrition), while the members of the remaining four divisions are normally provided with pigments which make holophytic nutrition possible, though many of these are also capable of heterotrophic nutrition and may therefore be described as "mixotrophic." In the lowest of the colourless groups in Senn's arrangement, the Pantostomatineæ, any portion of the body can ingest solid food by means of pseudopodia, while in all the remaining forms capable of holozoic nutrition such ingestion occurs only at certain definite points; the Pantostomatinean genus *Multicilia* has a spherical protoplast with numerous radially arranged flagella, but in all other Flagellata the body shows radial or bilateral symmetry, or may be asymmetrical, and the number of flagella is more limited. According to Senn, the Pantostomatineæ have given rise to the lower Protozoa (Sarcodina); to the small Flagellate group Distomatineæ with irregular bilateral symmetry and paired groups of flagella—this group forming a blindly-ending line; and to the very large group Protomastigineæ which comprises about half of the known genera of Flagellata and shows great variety in form and structure. The Protomastigineæ may be regarded as the common source of the Infusoria, Mycetozoa, Sporozoa, and perhaps also the Bacteria, on one hand, and of the four groups of pigment-bearing or "Algal" Flagellata on the other. Of these latter, the Chrysomonadineæ and the Cryptomonadineæ are, according to Senn, closely related but of independent origin; the Chrysomonadineæ have brown chromatophores, produce oil and leucosin, and show affinities with the Brown Algæ and the Diatoms, while the Cryptomonadineæ produce starch, are variously coloured or in some cases colourless, and may have given rise to the Peridiniales and the Green Algæ. The two remaining groups, Chloromonadineæ and Euglenineæ, differ from the other groups in having numerous green chromatophores; there is a more definite periplast or firm outer protoplasmic layer; the contractile vacuoles are so situated and co-ordinated as to form a pulsating system opening at a definite point on the exterior; the product of assimilation is oil (Chloromonadineæ) or paramylum (Euglenineæ). In the Chloromonadineæ, which Senn derives from *Monas*- and *Bodo*-like form among the Protomastigineæ, the contractile vacuoles are aggregated at the anterior end of the cell and open to the exterior by a pore. Senn regards the Chloromonadineæ as being too highly organised to serve as the starting-point for an Algal group as suggested by Luther and others (see below); but they have by further elaboration of the cell given rise to the Euglenineæ, a blindly-ending line representing the highest type of organisation found in the Flagellata and decidedly showing no Algal affinities, whatever may be said of the Chloromonadineæ. The Euglenineæ have, as compared with the Chloromonads, a more definite, often striated, and highly resistent periplast, and a gullet-like canal leading to a deep-seated vacuole into which a system of small and actively contractile vacuoles is drained.

Apart from Senn's compilation, the more comprehensive accounts of the Flagellata are contained in zoological works (18, 19, 37, 40, 93, 138, 150), and much of the recent literature on the "Algal" form is published in zoological journals. The Peridiniales will be dealt with in this review, since this group includes decidedly Flagellate forms, and reference will also be made to certain other groups (*e.g.*, Crystoflagellata, Silicoflagellata, Coccolithophoridæ) not classed by Senn among the Flagellata, though they occupy this position in zoological systems of classification. On the hand, the Trypanosomes and the majority of the other specialised heterotrophic Flagellata need not be considered in a discussion of the origin of Algæ from Flagellata.

In the following pages, it is proposed, taking as a starting-point the treatment of Algal groups in Engler and Prantl's Pflanzenfamilien and that of the Flagellata in the same work and in the more comprehensive zoological treatises, to review briefly the advances that have recently been made in our knowledge of certain lines of descent leading from Flagellata through transitional forms to the simpler Algæ. Restricting our speculations to such series as appear to include what may be fairly considered as transitional forms, we can recognise three main lines, leading (i) from the simpler Chloromonads to the Heterokontæ or Yellow-green Algæ; (ii) from the Polyblepharids to the Chlamydomonads and thence to the Isokontæ and other Green Algæ ? and (iii) from the Chrysomonads and Cryptomonads to the Brown Algæ, the Peridiniales, and probably certain other groups.

III—CHLOROMONADS AND HETEROKONTÆ ("CONFERVALES," "YELLOW-GREEN ALGÆ").

Until recently the Green Algæ have usually been divided into Conjugatæ, Protococcoideæ, Confervoideæ, and Siphoneæ—the division made, for instance, by Wille in Engler and Prantl's *Pflanzenfamilien* in 1890, and adhered to, with slight modifications, in that writer's recent supplement on the Chlorophyceæ in the same work (150). The Conjugatæ form a natural group, marked by the absence of ciliated reproductive cells—whence the name Akontæ given to the group in the modern system of Green Algæ based in part upon the ciliation of the asexual reproductive cells or zoogonidia—and by the siphonogamic sexual process of conjugation by means of a tube formed by the fusion of processes from the two gametangia. The limits and arrangement of the three remaining classes have, however, been considerably modified, owing chiefly to considerations advanced in publications by Chodat, Bohlin, Luther, and Blackman.

In all Green Algæ excepting the Conjugatæ (Akontæ), the zoogonidia and zoogametes are typically pear-shaped cells bearing at the anterior end a number of flagella. In most cases there are two (occasionally four) flagella of equal length inserted at the same point (Isokontæ); in the small order Œdogoniales the motile cells have a circlet of numerous flagella (Stephanokontæ); while in the Confervales there are two flagella of unequal length (Heterokontæ)—in some forms the shorter flagellum may, apparently, be absent. It may be added that in the attempts that have been made to connect Algal series with corresponding Flagellate series, the number and insertion of the flagella are not the sole criteria used, various other characters being taken into account. In certain groups of Flagellata, *e.g.*, the Euglenineæ, the flagella show considerable differences in genera which are obviously related closely to each other as judged by other cytological characters. When due attention is paid to the *tout ensemble* of characters, however, there can be little doubt that the flagellum characters (number, insertion, relative length where two or more are present) may afford a valuable clue to affinities.

In 1899, Luther (90) described a new genus, *Chlorosaccus* (Fig.

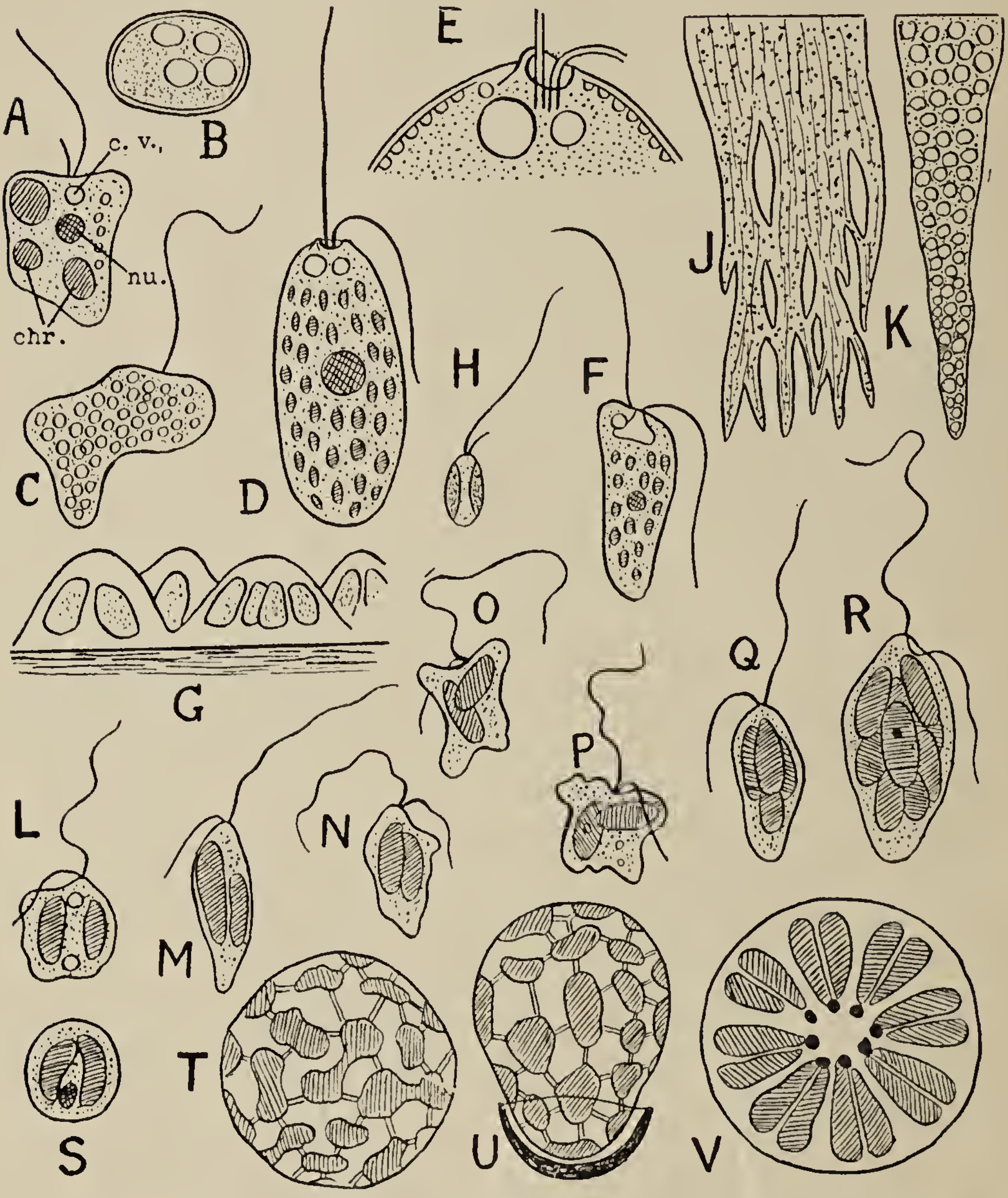


Fig. 1. CHLOROMONADINEÆ (Flagellate and Transitional Heterokontæ). A to C, *Chloramœba heteromorpha* Bohl.: A, a normal green individual, with nucleus, contractile vacuole, three chromatophores, and oil-drops; B, resting cyst; C, amœboid colourless individual. D, E, *Vacuolaria virescens* Cienk.: E shows the anterior end more highly magnified, with two vacuoles and insertion of flagella in the gullet-like pit. F, *Vacuolaria flagellata* Senn. G, H, *Chlorosaccus fluidus* Luther; G, portion of a colony; H, motile cell. J to V, *Leuvenia natans* Gardner; J, a portion of the floating colony; K, the same more highly magnified; L, a motile cell soon after being set free; M, N, O, P, later stages showing amœboid habit of the zoogonidia; Q and R, zoogonidia with four and eight chromatophores respectively; S, resting zoogonidium with the flagella withdrawn and with a cell-wall developed; a free floating colony showing the rapidly dividing chromatophores held together by protoplasmic threads; U, an earlier stage in development of colony, showing the ruptured cyst-wall at base; V, section through a young colony showing the nuclei and the chromatophores in pairs.

A—C from Bohlin; D, E, from Senn; F, from Stokes; G, H, from Luther; J—V, from Gardner.

1, G, H), which is of great importance as forming a connecting link between the Chloromonad genus *Chloramœba* (Fig. 1, A—C) on one hand and the Algal group "Confervales" on the other. This group had been previously founded as a distinct series of Green Algæ as the result of the work of Borzi (14, 15) and of Bohlin (10) on various genera which had formerly been included in the old groups of Protococcoideæ, Confervoideæ, and Siphoneæ. These genera differ from other Green Algæ in several characters besides the possession by the motile cells of two unequal flagella—namely, the presence of a large proportion of xanthophyll or carotin in their chromatophores (hence the name "Yellow-green Algæ" has been given to the group) which are typically numerous and discoid; the production of oil instead of starch as the visible anabolite; and the curious structure of the cell-wall in some genera, *e.g.*, the unicellular *Ophiocytium* in which the upper part of the wall becomes detached like a lid, and the filamentous *Tribonema* in which each cell is bounded by the halves of two H-shaped pieces and the whole filament readily breaks up into fragments of this shape. Luther and Bohlin concluded that these forms had arisen independently of the remaining Green Algæ, from the simpler types of the Flagellate group Chloromonadineæ, e.g., *Chloramœba*, through a transitional form like *Chlorosaccus*. On the other hand, *Chloramœba* leads through forms like *Vacuolaria* (Fig. 1, D—F) to the more specialised Chloromonadineæ and doubtless to the Euglenineæ, which need not be further considered here.

The genus *Leuvenia* (Fig. I, J to V), recently described by Gardner (48), appears to be related to *Chlorosaccus* and to form an interesting additional link in the chain connecting *Chloramœba* with the "Convervales." The motile cells are at first pear-shaped, with two unequal flagella and two ovoid curved green chromatophores (sometimes becoming four or eight by division); later the cell becomes amœboid. Growth occurs in a resting condition—the motile cells come to rest, float to the surface of the water, become spherical, withdraw their flagella, and grow rapidly in size; then the nucleus divides into as many as twenty, the chromatophores divide by constriction, and finally the whole interior divides up into zoogonidia, each appropriating two chromatophores and a nucleus. Under certain conditions the resting cells secrete a gelatinous substance causing them to adhere together in stringy floating masses, in which they become spherical; and in this palmella stage division into zoogonidia occurs as in the ordinary growth stage.

Pascher (112) has recently described a new genus of Heterokontæ (*Pseudotetraëdron*, which superficially resembles the Protococcaceous genus *Tetraëdron* but shows characteristic Heterokontan features—numerous discoid yellow-green chromatophores, production of oil instead of starch, cell-wall consisting of two portions fitting upon each other like a box and its lid.

Adopting the terminology suggested by Pascher (113), the following arrangement of the Heterokontæ may be proposed. It will be noted that the group is here divided into a series of orders which show a striking parallelism with the corresponding divisions of the Isokontæ. The genera of the Isokontan groups are omitted.

HETEROKONTÆ.	ISOKONTÆ.
Heterochloridales. *Chloramœba.* *Stipitococcus.*	Volvocales.
Heterocapsales. Heterocapsaceæ. *Leuvenia* (?) *Chlorosaccus.* *Racovitziella.* Botryococcaceæ. *Botryococcus.* *Askenasyella.* (?) *Oodesmus.* Mischococcaceæ. *Mischococcus.*	Tetrasporales.
Heterococcales. Chlorobotrydaceæ. Chlorobotrydeæ. *Chlorobotrys.* *Botrydiopsis.* *Polychloris.* *Centratractus.* *Pseudotetraëdron.* *Meringosphæra* (?) *Bohlinia* (?) Chlorothecieæ. *Chlorothecium.* *Characiopsis.* *Peroniella.* Sciadiaceæ. *Ophiocytium.*	Protococcales.
Heterotrichales. Tribonemaceæ. *Tribonema.* *Bumilleria.* *Monocilia.*	Ulotrichales.
Heterosiphonales. Botrydiaceæ. *Botrydium.* Vaucheriaceæ. *Vaucheria.* (?) *Dichotomosiphon.*	Siphonales.

(To be continued.)

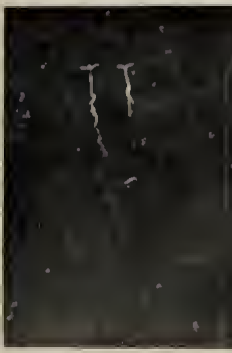


Fig. 1c.

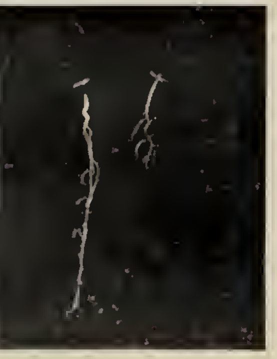
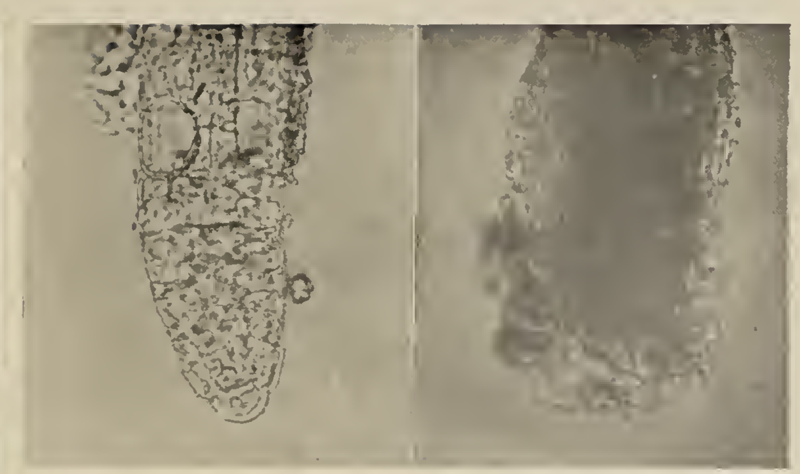


Fig. 1d.



a. Fig. 2. b.

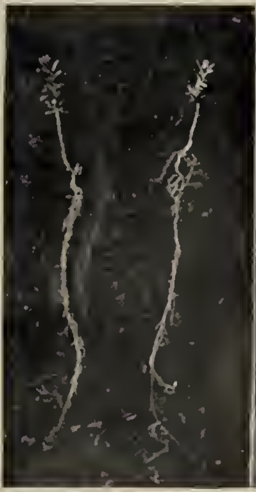


Fig. 1b.

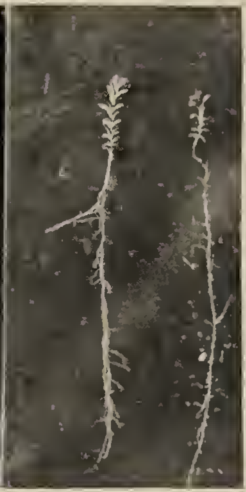


Fig. 1a.

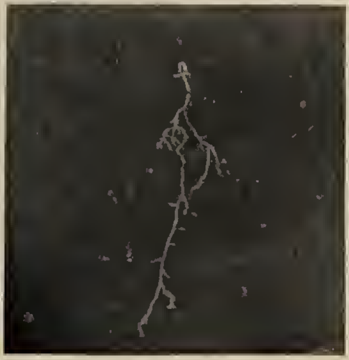


Fig. 5.

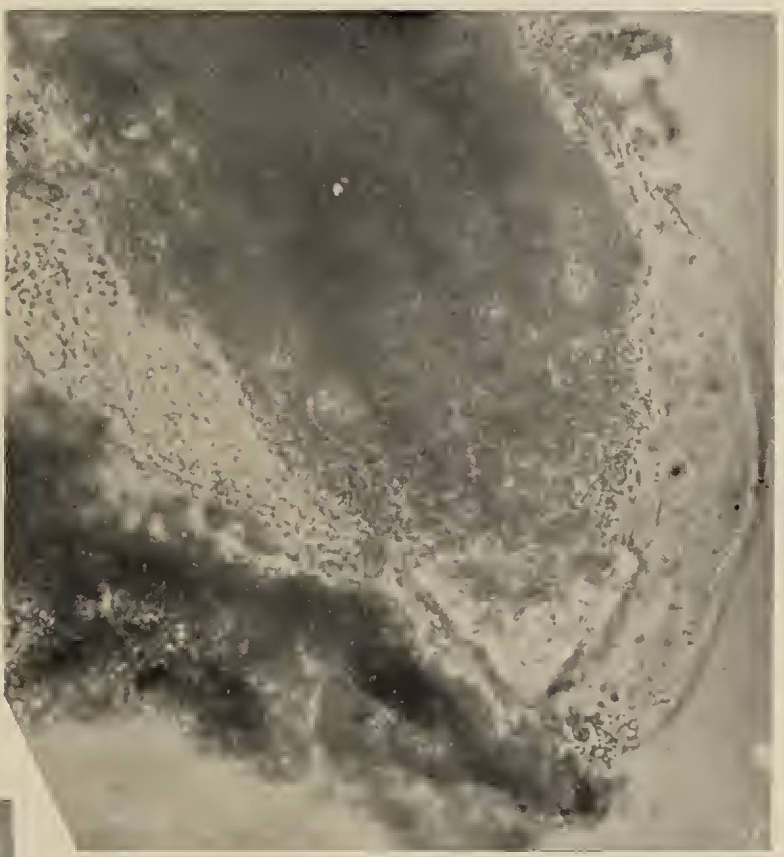


Fig. 3.

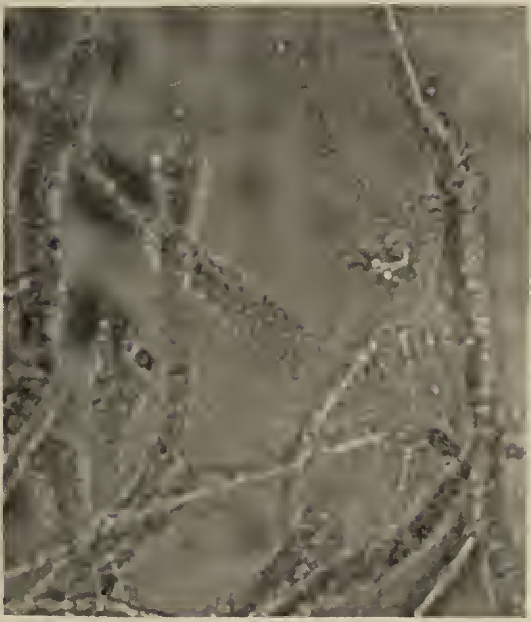
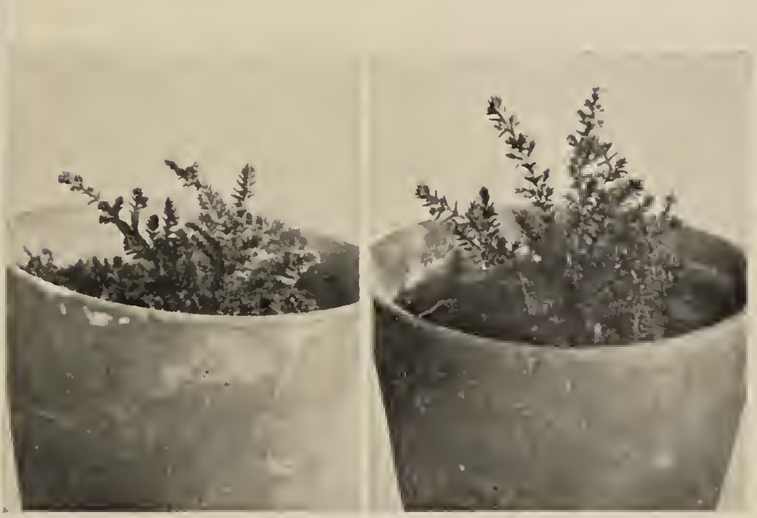


Fig. 6.



a. Fig. 4. b.

RAYNER.—ECOLOGY OF *CALLUNA*.

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THE VEGETATION OF JAPAN.

BY H. TAKEDA, D.I.C.

(Demonstrator in Botany, Royal College of Science, London).

I.—INTRODUCTION.

MANY valuable and interesting papers dealing with certain constituents of the flora of Japan have been published by not a few botanists, both Japanese and foreign. Yet there has been lacking, so far as I am aware, a general account of the flora or vegetation of Japan, except perhaps in the form of a catalogue or enumeration of plants growing in that Empire. It has been suggested therefore that a brief description of the vegetation of Japan would be interesting to the readers of this journal. The present paper has been re-written from lectures addressed in 1912 to the Natural History Society of the Imperial College Union and to the Botanical Society of London, and it is proposed therein to give a general idea of the vegetation of Japan.

II.—GEOGRAPHICAL FEATURES AND CLIMATE OF JAPAN.

The position occupied by Japan is somewhat similar to that of Britain, with this difference, that while the British Isles lie on the west of the European continent, the Islands of Japan are to the east of the mainland of Asia. Taking them in the order from north to south, the group of islands comprised in the present Empire of Japan consists of the Kurile Islands, the southern half of Saghalien, Yezo, the main island known to the Japanese as Hontô and occasionally called by Europeans Nippon, Shikoku, Kyûshû, the Loochoos, Formosa, and the Pescadores. These islands stretch diagonally from the 52nd down to the 21st degree of north latitude, and are situated between the 120th and 156th degrees of longitude east of Greenwich. The above described area of the Empire was increased in August, 1910 by the annexation of Corea, so that it has now much the same area[1] as that of Austria-Hungary, and the population[2] is nearly equal to that of Germany. A warm current called " Kuroshio", similar to the Gulf stream of northern Europe, originating between Luzon and Formosa, flowing past the eastern side of the latter and along the southern Loochoos, reaches the southern extremity of Kyûshû, where it divides into two branches. Whilst the main stream bends northward and flows along the south-east coast of Kyûshû, Shikoku, and Hontô, the smaller branch washes the west of Kyûshû and the Gotô group and runs up to the Sea of Japan through Tsushima or Krusenstern Strait. This so-called Tsushima Stream flows over the eastern half of the Sea of Japan from the south-west to the north-east and passes partly through Tsugaru Strait, but mainly through Lapérouse Strait, and soon dimishes when it reaches the southern part of the Sea of Okhotsk. The main division of the " Kuroshio " bends out into the Pacific Ocean about the 39th degree of latitude and takes a course towards the south of the Aleutian Islands and the coast of North America.

The cold currents in the northern Pacific Ocean, which affect the climate of Japan, originate partly in the Sea of Okhotsk and partly in the Behring Sea. The Kurile Stream, the most important of these, starts in the Penshina and Gishiga Bays and flows southwards along Kamtschatka, and then taking up a weaker current from the eastern side of this large Siberian peninsula, turns towards the Kuriles and washes the whole length of the chain of islands. The current then runs chiefly along the east-coast of Yezo, down to the 39th degree of latitude,[2] where the above-mentioned main stream of the warm current bends away into the Pacific Ocean. The water of this current is very cold and even in the summer its temperature does not rise above 5°C.

These warm and cold currents exercise great influence over the distribution of seaweeds. This is clearly seen on the east coast of Japan, the 39th degree of latitude being the separating point of two different algal floras. On the west coast, however, the course of the currents is more complicated, so that the elements of different floras appear somewhat intermixed, as will be seen from the following examples.

The strand-flora is similarly affected, the northern elements being distributed in the localities touched by the cold currents. To give some examples: *Mertensia maritima* is to be seen in the Okhotsk region, on the coast of Manchuria down to North Corea, while in the main island of Japan and especially on its east coast it is found northward from the 38th degree of latitude. Strictly speaking this plant, as it grows in the Far East differs, from the typical form of Europe and America, in having a stouter stem, and larger and more showy flowers, and it is recognised as a sub-species under the name of *asiatica.*[1] This sub-species is also found in various places on the Behring Sea. *Glaux maritima*, another arctic plant, which we meet with in various places in the British Isles, is distributed in Japan mainly from Yezo northward. But we also find this pretty seashore plant at a spot on the western coast of Hontô, whither the plant has probably been carried by the cold currents. *Plantago camtschatica* is another plant which is to be found in the localities visited by the cold currents.

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[1] 256,033 square miles. [2] 63,037,518. (Estimated in August, 1912).

[2] Occasionally it comes down as far south as the 38th degree.

The warm current has a similar influence on the distribution of plants; it is the important current by which our ancestors reached Japan in remote antiquity.[2] As this current comes into direct contact with the southern parts of Kyûshû, Shikoku, and Kii, various sub-tropical plants are found in these places. To give a few examples: *Rhizophora mucronata* is found at Kagoshima (32° N.L.); *Senecio scandens* in Tosa (Shikoku) and Kii; *Pteris Wallichiana* in Kii; *Asplenium Nidus* in Kii and the Gotô group; *Ipomœa biloba* (=*I. pescapræ*), in Echigo. *Statice japonica* which is mainly distributed in south-western Japan, is also to be found on the east coast as far north as the 38th degree of latitude.

Leaving the coast, let us now proceed inland and see what the country is like. The islands comprising Japan are all mountainous; there is no place from which we cannot see a prominent hill. Not a few of the smaller islands simply consist of one or more volcanoes. The great majority of the high mountains are densely clad with luxuriant vegetation from the foot right up to the summit—often so densely indeed, as to render the thick mountain-forests almost impenetrable. The mountains are generally lofty and exhibit the finest scenery of the country. The grandest mountain-chains are to be seen in Central Japan where they form the back-bone of Hontô, rising in places to an elevation of 10,000 feet. The higher peaks are made up partly of palæozoic, partly of plutonic, and partly of volcanic rocks. The youngest of the volcanic rocks, the andesite, broke not only through the various sedimentary rocks, but also through the granite, porphyry, and liparite. Although their altitude is so considerable, the mountains of Japan contain no glaciers, but slight traces belonging to an earlier period were discovered in 1902. There is, however, a great deal of névé present on some of the mountains. Mountaineering amongst the high peaks is very instructive, but the ascent is sometimes impeded by thick forest, so that it is necessary to follow a torrent, crossing it again and again until a waterfall intervenes, and then the bank has to be climbed. Sometimes the ascent is made by climbing a field of perpetual snow filling up a gully. Little mountaineering was done, except on certain peaks, until 1905, when the Alpine Club of Japan was organised. Since then very many men have spent their holidays amongst the mountains, climbing peaks where no educated person had been before, or following along huge mountain-chains, to find some new route, or discover new plants.

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[1] Cf. *Journ. Bot.*, 1911, p. 222.

[2] Said to have been some 3,000 years ago.

As the mountainous character of the country would suggest, Japan is naturally very rich in water. A dense network of rivers, torrents and lakes is to be seen nearly everywhere. With a few exceptions, the rivers are short and their gradient steep, causing frequent floods. In the late spring, when the snow which has gathered in the mountains during the winter, begins to melt, or when in the summer the continuous rain carried by the S.W. monsoon frequently falls in torrents, the water flows down in every mountain-furrow, and converts the small cheerful mountain-rivulet into an enormous stream. With the clashing of the muddy water, mixes the thundering sound of pieces of rock rolling over the bottom, carried down by the waves together with the lightly-built bridges and planks. Further down even the solid banks, carefully constructed on both sides of the wide stream, are not always able to withstand the power of the great mass of water or to check its work of devastation.

The numerous waters add a special charm to the magnificent woodland scenery of the mountains. The small stream, rich in trout, carries its clear waters in many directions, sometimes passing huge rocks adorned with pretty shrubs and ferns, sometimes spreading over a boulder, then narrowing into a rocky gorge shaded by bushes and foliage, here hurriedly setting over rocks and covered with white foam, there slowly winding round a projecting rock which appears to arrest its course. Where the water has hollowed out the bed, the purest blue green of the clear water may be enjoyed. It is generally considered in Japan, that a landscape is perfect only when water is present.

Very good examples of beautifully developed picturesque valleys can be seen amongst the greater archæan and palæozoic mountains. Here the various degrees of hardness and folding of the rocks offer a very unequal resistance to the weathering and eroding power of the running water.

It only remains now to mention the climate. As I have already pointed out, the Empire of Japan stretches over 30 degrees of latitude. Owing to this considerable length and the great variety in the orographic character of the country, uniformity of climate is out of the question, but to deal with this in detail would occupy too much space. In a word, the climate is much influenced by that of the neighbouring countries, and is modified by the warm and cold currents previously mentioned. The climate of the region from Formosa northward up to the mouth of the Amur River is practically under the control of the monsoons, which are formed by the warm damp south wind in the summer and cold strong north-west, north, and north-east winds in the winter. The Loochoos down to Formosa are sub-tropical and have practically no winter, while the Kuriles, the southern portion of Saghalien, which now again belongs to Japan, and certain parts of Yezo have the climate of Nova Scotia or Iceland. In the winter drifting ice is carried along by the currents and wind in the Kuriles and blocks up harbours, so that navigation is impracticable from November to April. On the northernmost islands of this chain, not until June does the snow disappear from the ground and vegetation then comes to life. Even in the north-east of Hontô, and especially in the so-called deep-snow districts, the snow lies on the ground during the winter some twenty feet deep, so that a whole village is often buried.

The rainfall is very large, and especially in the summer,[1] the air is very damp indeed, except in Hokkaidô (=Yezo and the Kuriles) which is not affected by the monsoon. The winter is dry and fine. The air is clear, the wind refreshing, and the sun bright. The seasons are very distinctly marked and the temperature is fairly even during each season. The annual range of heat and

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[1] An example of the rainfall in Tôkyô will be seen in the following table (in mm.):—

Jan.	Feb.	March	April	May	June	July
55·2	75·1	110·5	128·1	150·0	165·8	131·2

Aug.	Sept.	Oct.	Nov.	Dec.	Year
168·8	203·4	184·8	108·6	53·7	1475·2

cold is, however, much greater than in Britain; *e.g.*, in Tôkyô the mean temperature of the year is 13·8°C, the maximum being 36·6 and the minimum 9·2°.[1]

III.—COMPARISON AND ORIGIN OF THE FLORA.

Under such geographical, geological, and climatic conditions one expects to find a well-developed, varied, and abundant flora. This expectation will be realised, for the traveller meets with beautiful vegetation and an endless variety of plants throughout the country. Up to 1904 some 4,400 species of Cryptogams were recorded, and in the Index of Japanese Plants which has just been completed some 6,000 species of Phanerogams are enumerated,[2] we know, therefore, that there are not less than 10,000 species of plants indigenous to Japan. This number, however, does not include the plants of Saghalien and Corea, which came into the possession of Japan after the above-mentioned index was commenced.[3] An exhaustive survey of plant-species is not yet possible, for new species and varieties are constantly being published.

The flora of Japan belongs to Drude's Eastern Asiatic Region. Although the Empire is surrounded by seas, in the west it is closely connected with Manchuria through Corea, in the north it reaches Kamtschatca by the Kurile Islands, and Alaska through the Aleutian Islands, and also has a connexion with Amurland through Saghalien. On the other hand the Loochoos and Formosa join it to Southern China, the Philippines and the East Indian Islands. Thus, except on the eastern side, it is closely connected with other countries, and their respective floras show many signs of a close relationship with that of Japan.

It is rather difficult to say exactly when the archipelago of Japan separated from the Asiatic Continent, but there is evidence that Japan was connected with the mainland of Asia until a comparatively recent period. Plants indigenous in the eastern parts of Asia are also found in Japan. Teeth and various bones of the mammoth have also been discovered in several parts of the country.

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[1] An example of the mean temperature in Tôkyô is as follows (in C.):—

Jan.	Feb.	March	April	May	June	July
2·8	3·6	6·8	12·4	16·6	20·4	24·2

Aug.	Sept.	Oct.	Nov.	Dec.	Year
25·6	22·2	15·8	10·1	5·1	13·8

[2] Matsumura, Index Pl. Japonicarum, 1904—1912. The last volume of this Index includes but a few plants published after 1910.

[3] There are known more than 300 species of higher plants from the Japanese part of Saghalien, while in Corea there are roughly 2,150 species, of which about 200 are endemic. (The latter information was kindly supplied by Dr. T. Nakai, the author of *Flora Koreana*).

The characteristics of the flora of Japan in general are first the abundance of species and varieties, secondly, the presence of a large number of endemic species, thirdly, the proportion of woody plants is remarkably high, and lastly, the presence of tropical and sub-tropical elements throughout the country. Even in Yezo, the large island of North Japan, are found many representatives of southern floras, such as *Picrasma*, *Vitex*, *Rhus*, *Hydrangea*, *Lespedeza*, *Phellodendron*, *Aralia*, *Magnolia*, and others growing together with representatives of the cold flora. In the northern parts of Hontô, *Æsculus*, *Zanthoxylon*, *Ardisia*, *Elæagnus*, *Smilax*, and *Camellia* are often seen. The same or closely allied species have been found in the tertiary strata of the north of Eastern Asia. Probably in the middle of the tertiary period, even Saghalien had a much warmer climate, for at that time *Ginkgo*, *Biota*, *Sequoia*, and *Nilssonia* grew there. When, towards the end of the tertiary period, the greater part of the northern hemisphere was covered with ice, the main island of Japan seems to have suffered very little. Perhaps since the end of the glacial period and the change of climate in the middle diluvial age, Japan has maintained a fairly warm temperature, enabling many plants of warmer climates to survive, while in Saghalien the temperature has been very low, so that this island is unfavourable to plants of the warm temperate region. The arctic plants once compelled by the cold climate of the glacial period to come down southward were consequently left behind when the climate became warmer, but only persist on the summits of the high mountains.

Starting with the flora established in the tertiary period, the migration of arctic plants towards the south and of tropical plants towards the north has caused the present flora to be very complex. The connexion of the country with the northern, north-eastern, south-eastern, and southern parts of the Asiatic continent made paths for arctic and tropical plants into Japan. The interruptions between the various islands are bridged over to some extent by the currents and wind. The introduction of seeds might not have been successful, if the conditions of climate and soil had not been so favourable. Evergreen trees and shrubs and many other tropical plants found their way by degrees towards the north, and became acclimatized—so we may presume—to the colder winter night and contented with comparatively high temperature during the day, and above all the warm and moist atmosphere during the summer, when they can obtain their vital requisites. Those which came from the north or north-west, where they were accustomed to a severe winter, migrated up the mountains until they obtained the necessary climatic conditions.

Migrations must also have taken place in the post-tertiary period, for the great majority of the volcanoes were built up then, and also the irregularity of the surface of the country was to some extent brought about at this time.

From the results of investigations of the tertiary fossils of Japan, of Amurland, and of N. America, the conclusion may be drawn that the present flora originated in the large common flora of the northern region of the Far East. Its development to its present condition has already been elucidated. One striking feature is that the flora of the N.E. part of Japan bears a close relationship to that of the Atlantic coast of N. America. This was first noticed by Asa Gray a good many years ago. He endeavoured to compare the two floras and showed that more that 60% of Japanese plants grew on the E. coast of N. America, or if not, were represented by closely related species, while only 37% of these can be seen on the W. coast. He accordingly suggested that the close affinity between these floras originated in the tertiary period. Asa Gray's conclusion has been more and more firmly established as further geological evidence has accumulated, and consequently Engler and other geographical botanists have come to the conclusion that these two regions were actually connected, and had a similar climate and similar flora. After the glacial period many plants which migrated towards the south returned northwards and formed the foundation of the present flora of Japan, while in N. America, a change in climate had taken place between that of east and west. While in the west the climate became dry and mild and caused a great alteration in the flora, in the east very little change has taken place, and many old species have been preserved.

It should be borne in mind, however, that the vegetation of Japan, except that of the northern islands, has little actual resemblance to that of N. America. Although the same or closely allied plants occur in both regions, they are not found in the same proportion. For instance, in Japan *Tsuga* forms continuous and almost unbroken forests of great extent on the mountain slopes, above 5,000 feet from sea level, while in eastern N. America this tree is rarely found except scattered in small groves or as single individuals in the deciduous forests. On the other hand, *Picea* and *Abies*, which in America form immense forests almost to the exclusion of other species, in Central Japan grow singly or in small groves on the lower border of *Tsuga* forests or mingled with broad-leaved trees. In northern Japan and on the high mountains of Hontô, birches are more abundant than they are in the northern forests of America, and the river banks in the north, like those of N. Europe and Siberia, are lined with arborescent willows and alders, which are rare in eastern America, where these genera are usually represented by shrubs. This difference is due to the other dominant plants peculiar to each flora. The nnmber given in Gray's estimation should also be reduced slightly, since he included as natives some Chinese and Corean plants cultivated in Japan. Besides these and some endemic species, we have, as I have already remarked, a great many plants of the boreal region of the old world. For instance, *Asperula odorata* which occurs in Europe but not in America, grows abundantly in North Japan. In South Japan many tropical and sub-tropical elements may be seen. Certain plants growing in the central and southern parts of the country have also a close affinity to those of S. China as well as to those of the Himalayas.

IV.—Regions of Vegetation.

As has already been said, owing to the considerable length of the Empire, we cannot deal with the vegetation collectively, but are bound to divide it into certain regions. It may conveniently be arranged in three divisions mainly based on the climatic conditions:—(1) Northern, (2) Middle, and (3) Southern Regions. The Northern Region extends from the 38th degree of latitude northwards to the Kuriles and Saghalien. We may also include in it the northern part of Corea. The Middle Region is formed of the greater part of Hontô and Shikoku, a small part in the north of Kyûshû, and South Corea. The Southern Region includes the southern parts of the province of Kii and Shikoku, the greater part of Kyûshû, the Bonin Islands, the Loochoos, Formosa, and the Pescadores.

We must note here that within each of these regions there exists a certain degree of difference in the vegetation, according as we consider the northern or the southern portion. The northern part of the Northern Region is represented by the arctic, and the southern part by the sub-arctic, with a few elements of the cold temperate flora. In the northern part of the Middle Region the plants of the cold temperate flora are to be found, and in its southern part those of the warm temperate. The Southern Region possesses warm temperate and sub-tropical plants in its northern part, and tropical plants in the southern.

V.—PLANT-FORMATIONS.

In this chapter I intend to deal very briefly with various plant-formations. For the sake of convenience, the above-mentioned three regions are treated separately.

1. NORTHERN REGION. The sea-coasts of this region are lined partly with sand-dunes and partly with cliffs. In Hokkaidô, and especially in the Kuriles, sand-dunes are poorly developed. On the sand one generally finds *Amodenia* (*Arenaria*) *peploides* var. *oblongifolia*, *Arabis japonica*, *A. perfoliata*, *Matricaria ambigua*, *Atriplex patula*, *Carex macrocephala*, *C. pumila*, *Elymus mollis*, *Geranium yezoense*, *Inula Pseudo-Arnica*, *Lactuca repens*, *Linaria japonica*, *Lathyrus maritimus*, *Lilium dahuricum*, *Mertensia maritima* subsp. *asiatica*, *Phellopterus litoralis*, *Plantago camtschatica*, *Poa glumaris*, *Salsola soda*, *Thermopsis fabacea*, etc. In the sea we often come across *Phyllospadix Scouleri* and *Zostera pacifica*. Just inside the sand-dunes *Rosa rugosa*, which is very often cultivated in English gardens, forms thickets. Exposed parts of the cliff are often strikingly adorned with quantities of interesting arctic flowers, and even a small patch of rocks may form a beautiful garden. Some of the plants which we see here are as follows :—*Androsace Chamæjasme*, *Artemisia sacrorum*, *A. Schmidtianum*, *Chrysanthemum arcticum*, *Cochlearia oblongifolia*, *Conioselinum camtschaticum*, *Draba borealis*, *Empetrum nigrum*, *Erigeron subsuginosus*, *Fritillaria camtschatcensis*, *Hedysarum obscurum* var. *neglectum*, *Leontopodium kurilense*, *Ligularia sibirica*, *Lloydia alpina*, *Mertensia rivularis* var. *japonica*, *Oxytropis retusa*, *Parnassia palustris*, *Pedicularis venusta* var. *Schmidtii*, *Potentilla megalantha*, *Primula modesta* var. *Fauriæ*, *Rhododendron kamtschaticum*, *Salix arctica*, *Saxifraga bronchialis*, *S. cortusifolia*, *S. reflexa*, *Sedum camtschaticum*, *S. Rhodiola*, *Vaccinium Vitis-Idæa*, and so forth.

The salt-marsh, which is not a rare formation in N. Europe, is very feebly developed. There are only three or four localities known where *Salicornia* is found. But in rather muddy places near the sea, one often comes across the pretty *Glaux maritima* and *Triglochin maritimum*.

The dry hillsides are usually covered with *Miscanthus*, with which various species of *Artemisia*, *Aconitum*, *Convallaria majalis*, *Geranium*, *Hemerocallis Middendorffii*, *Lespedeza*, *Platycodon*, *Rumex*, and

Umbelliferæ. In humid places of the mountain valleys we often find *Artemisia vulgaris, Cacalia hastata, Lilium cordifolium, L. Glehni, Petasites japonicus, Polygonum sachalinense, Urtica platyphylla,* and so on, most of which are very robust.

The *Sphagnum* bog or "Hochmoor," which is not much in evidence in the other regions, is here fairly well developed. The following plants are frequently met with:—*Caltha palustris, Carex* spp., *Clematis fusca, Cornus suecica, Drosera rotundifolia, Eleocharis* spp., *Eriophorum alpinum, E. vaginatum, Gentiana jesoana, Ledum palustre* var. *dilatatum, Lonicera cœrulea, Lycopodium clavatum, L. inundatum, Lysichiton camtschatcense, Molinia cœrulea, Myrica Gale* var. *tomentosa, Oxycoccus palustris, Phalaris arundinacea, Scheuchzeria palustris, Scirpus* spp., *Trientalis europæa* var. *arctica*, etc. In the early summer when the silky cotton-grass displays its beauty, blue Irises (*I. lævigata* and *I. setosa*) take their part in adorning the swamp. Pretty orchids such as *Arethusa japonica* and *Pogonia japonica*, the blue *Gentiana Thunbergii*, the tall *Viola Langsdorffii*, and the white *Spiræa betulifolia*, present a delightful sight. Tall Umbelliferæ such as *Angelica* and *Heracleum*, which remind us of the scenery of the arctic vegetation, line the margin of the swampy places in the summer, but in the autumn these are replaced by the huge *Senecio palmatus* with yellow flowers, and the deep blue *Gentiana jesoana* is fully open.

In the ponds and lakes one often sees *Hippuris vulgaris, Polygonum amphibium, Potamogeton natans, P. perfoliatus*, with which *Fontinalis, Lemna trisulca* and *Utricularia minor* are occasionally associated.

In the deciduous woods, on hillsides, and even on the fairly high mountains, *Sasa paniculata, S. kurilensis* and *S. nipponica* are very abundant. These bamboos have comparatively thin culms and broad leaves, and form very dense thickets, under which various shade-loving plants find protection.

The characteristic forest trees are the deciduous oaks (*Q. dentata, Q. glandulifera*, and *Q. grosseserrata*), birches (*B. alba, B. Ermani, B. Maximowicziana*), cherries (*P. Maximowiczii*, and *P. serrulata*), elm (*U. japonicus*), hornbeam (*C. cordata*), maples (*A. japonicum, A. Mayri*, and *A. pictum*), poplars (*P. suaveolens* and *P. tremula*), and *Cercidiphyllum japonicum*. The last-named is a very peculiar tree, the sole representative of the family Cercidiphyllaceæ. Its general appearance closely resembles that of *Ginkgo*, so that it has often been mistaken for the latter by casual travellers.[1] Various kinds of *Salix* are very often found in more or less damp places. Conifers are not rare, but comparatively few species are present, e.g., *Abies Mariesii*, *A. sachalinensis*, *Juniperus chinensis* var. *procumbens*, *Larix dahurica*, *L. kurilensis*, *Picea ajenensis*, *P. Glehni*, and *Taxus cuspidata*. Pines are rare except in cultivation. The only wild species is *P. pumila* which is usually three or four feet, occasionally five to seven feet in height, and generally grows on mountain summits. *Thujopsis dolaborata*, one of the finest Conifers, grows to a great size in the southernmost part of this region.

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[1] cf. Hemsley, Ind. Fl. Sin. ii, p. 547; also *Ann. Bot.*, xiv, p. 119.

Even in Saghalien and the Kuriles we often meet with several woody climbers, such as *Actinidia arguta*, *A. Kolomikta*, *Celastrus articulatus*, *Hydrangea scandens*, *Rhus Toxicodendron* var. *radicans*, *Vitis Thunbergii*, etc., which grow in tropical luxuriance. Not only here, but also in other parts of Japan, we frequently find many woody climbers. Sargent attributed this fact to the abundant undergrowth of bamboos, which cuts off most of the light, and makes the plants climb up the trunks of other trees.

On the high peaks which are not much more than 7,000 feet in altitude, we find many interesting arctic plants such as *Bryanthus* and *Phyllodoce* generally growing on exposed rocks.

The vegetative period of this region is very short. Still, as soon as the spring arrives, everything is quite ready for rapid growth, and before September comes with the keen autumn wind, seeds are set and dispersed.

2. MIDDLE REGION. This region is very extensive and mountainous, so that the vegetation is not uniform.

The coasts are beautifully lined with graceful pine trees. *Pinus Thunbergii*, which is well adapted to sandy sterile localities, is the species most often found on the sea shore. The following plants are some of the representatives of the sand-dune plants:—*Amodenia peploides* var. *oblongifolia*, *Arabis japonica*, *A. perfoliata*, *Artemisia Fukudo*, *Arundo donax*, *Bœhmeria biloba*, *B. holosericea*, *Calystegia Soldanella*, *Carex macrocephala*, *C. Pierotii*, *C. pumila*, *Cinidium japonicum*, *Crepis lanceolata*, *Crinum asiaticum* var. *declinatum*, *Corydalis platycarpa*, *Dianthus japonicus*, *Fimbristylis spathacea*, *F. velutina*, *Ischæmum anthephoroides*, *I. Sieboldii*, *Lactuca repens*, *Lathyrus maritimus*, *Linaria japonica*, *Lubinia lubinioides*, *Phellopterus littoralis*, *Rhaphiolepis japonica*, *Samolus floribunda*, *Sedum oryzifolium*, *Statice japonica*, *Vitex trifoliata* var. *orata*, *Wedelia procumbens*. Rocky cliffs are infrequent, nor do they present a gay appearance as they do in the Northern Region. The species growing in this sort of locality are comparatively few, such as *Chrysanthemum Decaisneanum*, *C. marginatum*, *Cotyledon* spp. *Sedum* spp., *Polystichum falcatum*, and so forth.

The forest trees of this region are of great variety. Evergreen trees occur largely and broad-leaved species are especially numerous. In the spring trees and shrubs with conspicuous flowers such as different kinds of *Azalea*, *Prunus* and *Pyrus* decorate the woods on every hand, and in the autumn the foliage of various deciduous trees displays gorgeous hues. More species of *Pinus* appear in this region, and *Cryptomeria*, one of the most beautiful trees in Japan, flourishes here. The tall bamboos, mostly belonging to the exotic genus *Phyllostachys* add a special feature to the vegetation. They are almost exclusively under cultivation, and form dense groves. The largest of them (*P. edulis*) exceeds 30 feet in height, the base of the culm measuring as much as 10 inches in diameter.

The uncultivated fields, which are called "hara" in general, are usually covered with a dense growth of *Miscanthus* and other grasses, amongst which grow small shrubs and thousands of herbaceous plants, including the fine *Lilium auratum*, that prefer dry sunny situations.

This middle region contains the huge mountain ranges with perpetual snow lying in the gulleys, of which I have already spoken. The flora of these mountains generally presents zones of different vegetation, as we ascend from below to the summit.

Taking Mount Fuji, which is the highest volcano in Japan, and is moreover the world-famous "peerless mountain", as a type, we shall find the mountain-flora of a temperate country. This peak stands practically on a plain, and if one likes, one can start climbing from the very seashore. Supposing we take a village at the southern base of the mountain as a starting point, then we shall ascend, first of all, a long gentle slope. This is composed of lava and cinders, and is almost useless for cultivation. Various sorts of grasses, *Rubi*, wild roses, and bracken cover this wide area, and small shrubs and trees grow in scattered spots. In the summer thousands of herbaceous plants with yellow, pink, blue, white or purple flowers convert the wilderness into a splendid flower garden, where one often comes across many a gorgeous butterfly. Small patches of alluvial soil deposited by the action of water are seen here and there. In such places many interesting trees such as *Abies* *firma*, *Acer* spp., *Castanea sativa*, *Cephalotaxus*, *Cinnamomum Camphora*, *C. pedunculatum*, *Cryptomeria japonica*, *Diospyros Kaki*, *Eurya japonica*, *Larix leptolepis*, *Listea aciculata*, *L. glauca*, *Pasania cuspidata* and *Quercus* spp. are to be found, partly wild and partly planted.

At the 3,000 feet level the basal zone which we have just passed, begins to show a transition to the tree zone. The tree zone may be divided into the deciduous tree belt and the conifer belt, the former taking the lower part and the latter occupying the upper portion. The broad-leaved trees growing here include the following:—*Acer*, *Alnus*, *Betula*, *Carpinus*, *Cercidiphyllum*, *Cornus*, *Corylus*, *Euptelea*, *Euonymus*, *Hydrangea*, *Quercus*, *Stephanandra*, *Viburnum*. Very many shade loving plants form the undergrowth. In the conifer belt, *Abies firma* appears first, and this is followed by *Larix*, *Picea*, *Tsuga*, and other species of *Abies*. Mosses and liverworts form a thick cushion on rocks and trunks, and with these occur a number of interesting ferns and orchids.

When we reach the 6,000 feet level, the gradient becomes much steeper, and trees are less abundant. The mountain ash, *Rhododendron*, *Alnus* spp., stunted birches, shrubby *Spiræa*, dwarf willows and various ericaceous shrubs remind us that we are reaching the shrub zone. The flowers we meet with here are mostly of alpine character. Species of such genera as *Adenophora*, *Arabis*, *Artemisia*, *Astragalus*, *Clematis*, *Geranium*, *Patrinia*, *Polygonum*, *Stellaria*, and *Thalictrum* are quite different from their congeners growing down below.

The zone between 7,500 feet to 10,000 feet from sea-level belongs to the Alpine region. Plants growing in this zone are typically alpine and arctic. *Arabis serrata*, *Artemisia pedunculosa*, *Astragalus membranaceus*, *Clematis alpina*, *Hedysarum esculentum*, *Polygonum cuspidatum* forma *colorans*, *Stellaria florida* var. *angustifolia*, *Vaccinium Vitis-Idæa* are the plants which commonly occur here.

Above this up to the summit, which is about 12,450 feet above sea-level, is the Lichen zone, where one comes across various lichens such as *Cetraria islandica* forma *angustifolia*, *Cladonia rangiferina*, *Rhizocarpon geographicum* and *Stereocaulon octomerum*. Here and there those plants which we have seen in the Alpine zone grow in crevices of the lava, but they do not thrive as they do some way further down.

Practically the whole area of the summit is occupied by a large crater not far short of 2,000 feet in diameter, which is surrounded by a series of small rugged peaks. Two springs of very pure cold water supply the demands of crowds of mountaineers.

The Alpine zone of Mount Fuji does not contain many plants, though there are a few things only known from this mountain. On the other mountains of Central Japan, which form the back-bone of the main island, and are often called the Japanese Alps, the Alpine vegetation is very well developed. On these mountains a creeping pine, *Pinus pumila* which also occurs in Siberia, appears in the shrub zone, and extends to the Alpine zone. The thickets of this pine are very troublesome to cross, but under their shade various interesting plants are found, *e.g.*, *Coptis trifolia*, *Fritillaria camtschatcensis*, *Linnæa borealis*, *Lycopodium alpinum*, *L. Selago* var. *appressum*, *Listera cordata* and other orchids, *Rubus pedatus*, *Viola biflora*, *V. crassa*, and so forth. Many arctic plants which occur on the rocky cliffs of the Kuriles can also be found in the Alpine zone of these mountains. One of the most attractive things is *Dicentra pusilla*. This plant is about a span high, with much dissected, intensely glaucous leaves, and a terminal raceme bearing some half-a-dozen large pink flowers. A beautiful sight is a carpet made up of the crimson flowers of *Primula cuneifolia* with white patches of *Anemone narcissiflora*. Mosaics of the crimson *Geranium yezoense* var. *nipponicum*, the golden-yellow *Ranunculus acris* var. *Steveni* and *Trollius patulus*, and the blue *Aquilegia siberica* var. *flabellata* are another sight of the Alpine zone. On the rocks we occasionally find *Campanula lasiocarpa*, *C. pilosa* var. *dasyantha*, *Diapensia lapponica* var. *obovata*, *Empetrum nigrum*, *Eritrichium nipponicum*, *Geum calthaefolium* var. *dilatatum*, *Hypericum camtschaticum*, *Lloydia alpina*, *Saxifraga bronchialis* var. *cherlerioides*, *Sedum Rhodiola* var. *Tachiroei*, and so on. In the crevices of the rocks the very peculiar looking *Cassiope lycopodioides* grows, while its congener *C. Stellariana* prefers a moist place. *Dryas* is very rare, and is known only from four or five localities, but it is replaced by a member of the same family, namely *Geum dryadoides* which has white flowers and bearded achenes. The species of *Ranunculus* with white flowers are totally unknown from the Japanese Alps, while *Soldanella* is replaced by a member of the Diapensiaceæ called *Shortia soldanelloides*. Neither *Cyclamen* nor *Sempervivum* grow in any part of Japan. One of the rare and interesting plants is *Anemone Taraoi*,[1] with a pale yellow flower, which though it has a similar appearance to *A. sulphurea*, belongs to a different subgenus. This plant is endemic to Japan and occurs only on the summits of a few high mountains and in the Kurile Islands. When, in the late summer or early autumn, the frost has made the leaves of *Arctous alpina* bright red, a mountaineer will enjoy ripe fruits of various species of *Vaccinium*, *Prunus*, *Lonicera*, and *Empetrum*. In rather dry sandy places one often finds species of *Adenophora*, *Arnica*, *Draba*, *Euphrasia*, *Gentiana Loiseleuria*, *Oxytropis*, *Potentilla*, and some grasses such as *Deschampsia* and *Festuca*, while in humid localities *Alchemilla*, *Fauria*, *Pedicularis*, *Phyllodoce*, *Sibbaldia*, *Swertia*, *Tofieldia*, and *Veratrum* are to be found. The ferns growing on the rocks are few, but elegant, and include *Asplenium viride*, *Cryptogramme crispa*, *Polystichum Lachenense* and *Woodsia ilvensis*. While most of these ferns occur in Europe, the *Polystichum* is only known from the Himalayas. *Botrychium Lunaria*, not at all uncommon in Europe, is comparatively rare in Japan, and *B. lanceolatum* is perhaps the rarest. A good many new species of plants have been discovered and described from the Japanese Alps, while many known species have been found and added to the flora. On the whole the Alpine flora of Japan is mostly composed of arctic plants, some of which are not seen on the European Alps.

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[1] For a description, see *Journ. Bot.*, 1910, p. 266.

Finally the aquatic vegetation of the middle region may be mentioned. There is a great diversity in the representatives of aquatic plants. The commonest genera which we find in nearly every pond, ditch, or lake are perhaps as follows:—*Alisma*, *Ceratophyllum*, *Hydrilla*, *Hydrocharis*, *Lemna*, *Monocharia*, *Myriophyllum*, *Nuphar*, *Nymphaea*, *Ottelia*, *Phragmitis*, *Potamogeton*, *Rotala*, *Sagittaria*, *Scirpus*, *Trapa*, *Typha*, *Utricularia*, *Vallisneria* and *Zizania*. Besides these flowering plants, water ferns such as *Azolla*, *Marsilia*, and *Salvinia* occur in the stagnant water. *Isoetes japonica*, which is one of the largest species of this genus, is to be met with in running water in certain places.

3. SOUTHERN REGION. We will now pass to the Southern Region, where, even at its northern limit, Kyûshû, the vegetation is quite sub-tropical. Particularly on the sea-coasts, which are washed by the warm current, various Indo-Malayan strand plants are to be met with. In the Loochoos, *Bruguiera gymnorhiza* forms the mangrove-forest in the tidal estuaries. Well-developed mangrove-forests are to be seen in Formosa, which are composed of

Avicennia officinalis, Kandelia Rheedii, and *Rhizophora mucronata.* In such marshy places one finds such plants as *Halophylla, Scævola,* and *Suæda australis.* On the sandy beach we often get *Barringtonia* spp., *Cassytha filiformis, Ipomœa biloba, Pandanus* spp., *Peperomia portulacoides, Vigna lutea* and so forth. Various palms belonging to such genera as *Arenga, Livingstonia, Trachycarpus,* and so on, flourish in the Region.

This is really a region of *Ficus,* with which broad-leaved evergreen trees and shrubs such as various Lauraceæ, *Quercus, Hibiscus, Myrica rubra,* etc. are found. On their branches a great many epiphytic orchids, lycopods and ferns, and sometimes parasites such as *Loranthus* spp. and *Viscum japonicum* are found. In the dense moist forests many tropical ferns such as *Allantodia javanica, Alsophila,* spp., *Angiopteris evecta, Cyathea, Dicksonia, Gleichenia* spp., *Osmunda javanica, Pteris quadriaurita, P. wallichiana* flourish. Amongst other woody climbers I may mention the occurence of *Bauhinia japonica* in Kyûshû. In the Loochoos we get more tropical plants such as *Garcinia, Pinus luchuensis, Terminalis Katappa* and others. The famous *Cycas revoluta* thrives very well in these islands, and from its pith a sago is prepared. Various interesting orchids and ferns including *Helminthostachys zeylanica* are also to be met with.

If we pass over the Loochoos and come to Formosa, the vegetation is typically tropical. Although the climate is not uniform throughout the island, huge trees, thick bushes, dense forests with a great number of woody climbers can be found everywhere. In the mountain valleys we frequently come across *Cinnamonum camphora,* from which the camphor of commerce is obtained, reaching huge dimensions. *Macuna gigantea* and *Pusætha scandens,* both famous for their tremendous legumes, other climbers such as the Lotung, and gigantic bamboos, tall tree ferns, palms, and the wild *Musa* grow in the forests and on mountain-slopes. If we go higher up on the mountains which occupy the greater part of the island, we shall see conifers at an elevation of about 6,000 feet above sea-level. *Chamæcyparis formosensis, Cunninghamia Konishii, Picea morrisonicola,* and *Pinus formosana* are some of the interesting species, and are only known from this island. A few years ago a new genus of conifer was discovered amongst the mountains, about 6–8,000 feet above the sea. The external appearance of this tree is somewhat similar to that of *Cryptomeria,* so that people thought at first that they had found a wild *Cryptomeria*, until the cone was obtained and closely examined. Then the plant proved to be a new genus and was accordingly named *Taiwania cryptomerioides* in honour of this beautiful island. The systematic position of this genus was suggested to be between *Athrotaxis* and *Cunninghamia;* further investigations, both anatomical and cytological, are much to be desired.

Higher up on the mountains we first get the shrub-zone and then at an elevation of 12,000 feet and upwards various plants of alpine and arctic character, such as *Arabis*, *Artemisia*, *Cerastium*, *Deschampsia*, *Festuca*, *Fragaria*, *Gentiana*, *Gnaphalium*, *Leontopodium*, *Luzula*, *Potentilla*, *Shortia*, *Sibbaldia*, *Trisetum subspicatum*, and so forth.

If we go down to the southernmost part of the island, we shall everywhere meet with nothing but real tropical plants, and the vegetation shows a close relationship to that of the Philippines, India, and Java. Certain elements belonging to Cochin-China and of southern China will also be detected.

Roughly speaking, there are some 2,500 species (belonging to some 770 genera) of higher plants known, 17% of which are endemic; and many more will be discovered in the future in this island which promises so much to the enthusiastic botanist.

VI.—Cultivated Crops.

A few words may perhaps be added on this subject. The most important plant is undoubtedly the rice-plant, *Oryza sativa*, with a great many cultivated varieties and races. The plant is grown throughout the country with the exception of Saghalien and the Kuriles. Particularly in Central and S.W. Japan, every possible piece of land is converted into rice-fields, which present a very striking feature to the eye familiar only with European scenery. A rice-field is, in a word, a muddy swamp divided up by low narrow banks into more or less square areas. The plant is raised in the nursery and seedlings of about a span high are transplanted from this into the rice-field proper. In the summer the rice-field is of a delightful green colour; in the autumn it turns somewhat golden, as the grain ripens and the plant withers. In the winter, after the harvest, the rice-field looks quite desolate, but often furnishes the best shooting-ground for snipe and other game-birds. Sometimes the rice-plant is also grown in dry fields where water is not available.

In Saghalien and the Kuriles, the temperature is very low during more than half the year, so that cultivation is hardly to be hoped for. The vegetation of these districts is little touched by human hands, so that the original features are exceedingly well seen.

In Yezo, except perhaps its eastern parts, the temperature rises considerably in the summer, so that various sorts of grain and vegetables are produced, and especially excellent varieties of apple. The cultivation of the hop and flax, which meets with considerable success, may also be mentioned.

In the Middle Region, plains and small hills are cultivated with rice, other grains, beans, peas, cucumber, egg-plant, radishes, turnips, mustard, *Lagenaria*, *Colocasia antiquorum*, potatoes, sweet potatoes, and so forth. Besides these vegetables one often comes across the cotton-plant, hemp, tobacco-plant, and mulberry, the last of which is utilized for sericulture. Various fruit-trees such as apricot, fig-tree, peach, pear, persimmon, orange, vine, and *Eriobotrya* are also grown. Nor must I omit to mention the tea-plant, and paper mulberry and *Edgeworthia* for paper manufacture. Various species of the bamboo, *Phyllostachys*, which, as already said, form a peculiar feature in the warmer parts of Japan and were probably introduced from China at an early period, yield valuable material for various purposes. Fences, pegs, baskets, arrows, trellis-work, hoops for barrels, shafts of umbrellas, cages, and fishing rods can be made out of the culm, while the sheath of the young shoot is useful for wrapping or for making hats or sandals. There are a good many species of bamboo, belonging to *Arundinaria*, *Bambusa*, and *Sasa*, used for similar purposes, or much valued as ornamental plants. A species of *Dendrocalamus*, from which a kind of paper can be manufactured, grows in Formosa.

As a matter of course sub-tropical and tropical crops are grown in the Southern Region. In addition to those mentioned above in the Middle Region, there are such plants as bananas, coco-nut, pineapple, and sugar-cane. *Musa luchuensis* yields a fibre of good quality, while an excellent kind of hat can be made out of the leaves of a screwpine. *Tetrapanax papyrifera*, from the pith of which the so-called rice-paper is prepared, grows in Formosa.

VII.—INTRODUCED AND GARDEN PLANTS.

In this last chapter I may perhaps deal briefly with gardening and garden plants.

Gardening must have been introduced from China together with other arts and especially with Buddhism. Buddhist priests may have been the first to construct gardens after the Chinese patterns, which was greatly modified in later years. So far as I know, one of the famous gardens, designed some 500 years ago, still exists.

Generally speaking, the gardens are very different from European ones. Geometrical carpet bedding and lawns are quite unknown, and beds are used only in the nursery. Rather different from the original Chinese gardens, which are more artificial and Gothic, the Japanese gardens are miniatures of natural landscape. Generally, there is a small hill or two, a pond, a bridge, and a few stone lanterns. This is copied (very badly) on a small scale and exhibited at the Temple show every year. Trees and shrubs are mostly used, and comparatively few herbaceous plants are grown. Pines and *Chamæcyparis* are indispensable. Except *Abies firma*, which is hardy in the lowlands, other species of this genus and *Picea* are hardly ever seen, while a dwarf variety of *Taxus cuspidata* and *Juniperus chinensis* are sometimes used. Broad-leaved evergreen trees and shrubs are mixed with deciduous plants. Half-a-dozen species of *Prunus* are planted for the sake of their flowers, while a great many varieties of *Acer palmatum* and other species of maple are grown for their foliage. Ferns are usually neglected except for a few hardy species. Amongst shrubs many kinds of *Azalea*, with *Cydonia*, *Nandina*, and *Pyrus floribunda* are favourites, while *Wistaria* is often planted over a pond. Stones and rocks of different colour and shape are always placed in certain definite positions, and sometimes even a small cascade is reproduced falling over a rock. There are several types of gardening, the principles of which are not very easily understood; some trees, shrubs, and stones should occupy a certain position, trees should have certain ramifications, and certain shrubs should be trimmed in definite ways.

In some cases, a landscape garden is skilfully reproduced in a box or in a pot. One of the best examples which was transferred from the Japan-British Exhibition can be seen in Battersea Park, London. For this purpose the plants used must necessarily be small, but perfect in style and shape.

The dwarf pot trees, which appear somewhat mysterious, even to a scientific eye, may also have been introduced from China. The art has been improved with great skill. Not only arboreal plants, but also various other evergreen plants such as *Acorus gramineus*, *Rhodea japonica*, and even *Psilotum triquetrum* became material for pot cultivation. Some are grown for their flowers, others for fruit, or foliage. In some years variegated leaves of any plant are much valued, in other years *Chamæcyparis* is in fashion, and so forth.

Curiosity drove people into little explored parts of the country to discover curious or unusual plants for this purpose. Also, very many plants were imported from China and Corea or even from the tropics. The introduction of foreign plants took place not only in recent years, but in ancient times for economic, pharmaceutical, and other purposes. *Cryptomeria japonica*, for instance, which is so widely cultivated all over the country, is said to have been imported from Corea in prehistoric times. Rice and various other grains must have been brought by our ancestors from somewhere abroad. History tells us that the orange, or at any rate a kind of orange, was imported for the first time in the year 70 A.D. The Corean medical art was introduced into Japan in 510, and with this came also pharmaceutical botany. In 701 a physic garden was established, and medical botany was taught there. Afterwards very many plants possessing medical value were introduced from China and Corea, and in later years many economic and garden plants also. Sometimes the introduction was made quite by chance, *e.g.*, in 799 a foreigner is said to have arrived in Central Japan, having drifted ashore on the waves, and he brought with him some seeds of the cotton-plant.

These introduced plants were not always indigenous to China or Corea. The Chinese imported various plants into their own country from their southern and western neighbours ; *e.g.*, according to the history of the Han, the Chinese General Chang K'ieng who was despatched about 139 B.C. by the Emperor Wu on a diplomatic mission to a neighbour living to the north-west of China, brought back the vine from western Asia about 120 B.C. After the discovery of America, very many American plants were introduced by the Spaniards and Portuguese into the Philippines and the East Indian Archipelago. Their cultivation spread rapidly over the neighbouring parts of the Old World, and they found their way also into China. These plants may possibly have been imported into Japan directly or through China, and throve there equally well with the indigenous forms.

The first European who came over to Japan and made a botanical collection was Andreas Cleyer. He came with a Dutch Ambassador about 1675, and stayed in Western Japan four years. Afterwards he published a book containing illustrations of 1,360 species of plants. Then George Meister who knew Cleyer arrived in Japan in a similar manner, and published in 1692 an account of his journeys and observations. Just after him, in 1690, Engelbert

Kaempfer reached Japan and stayed three years. He was the first to illustrate *Ginkgo* in his book published in 1712. After some ninety years, Thunberg who was a pupil of Linnaeus came over to Japan, studied the plants and published his *Flora Japonica* in 1784. He also published an account of his journeys and illustrations of some Japanese plants. I am not quite certain if these people brought back seeds or plants from Japan, but there is no doubt about Von Siebold who came over some forty years later, and took a few living animals and plants away with him.

Robert Fortune, who paid repeated visits to China during eighteen years from 1843, sailed to Japan in 1860 and again in 1861.[1] He saw a number of interesting plants there and introduced several garden plants. About the same time John Gould Veitch went over to Japan for the purpose of obtaining garden plants, and introduced a great many plants into English gardens in 1861. Amongst others the following few are perhaps worthy of note:—*Adiantum Veitchii* (=*A. monochlamys.*), *Ampelopsis Veitchii* (=*Parthenocissus tricuspidata*), *Abies Veitchii*, *A. Alcockiana*, *Cryptomeria japonica* var. *elegans*, *Lilium auratum*, *Picea ajanensis* var. *microcarpa*, *Polypodium Veitchii*, *Primula cortusoides* var. *elegans* (=*P. Sieboldii*), *Selaginella involvens* var. *Veitchii.*

Messrs. Standish and Noble of Bagshot Nursery were the first to cultivate the new Chinese plants discovered by Fortune. They also received the following Japanese plants obtained by that distinguished collector:—*Aucuba japonica*, *Deutzia crenata*, *Tricyrtis hirta*, etc.

J. G. Veitch was followed by Maries who also collected many dried specimens which are now preserved at Kew, and I have had an opportunity of examining and naming some of them.

These people saw in Japan very many interesting and curious plants and certainly thought all of them were indigenous to Japan, and a number of the new species were named "japonica." In fact some of these are not true natives of Japan, but are merely cultivated in the gardens. For instance, *Cydonia japonica*, generally known under the name of "japonica" in this country, is of Chinese origin. *Eriobotrya japonica* which is so much grown on the northern coasts of the Mediterraneans, is probably not a native of Japan. *Mahonia japonica* is another plant, which was described from a specimen grown in a Japanese garden, was introduced into

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[1] The narratives of his journey were published under the title of "Notes on the Botany of Japan" in *Gard. Chron.*, 1861, pp. 145, 312, 385, 456, 576, 737.

Japan in 1684 probably from China, where until to-day no true *M. japonica* has been collected, but an allied plant occurs, *M. Bealei*, which has been taken for the other one in this country. The beautiful garden Chrysanthemum, which is the national flower of Japan, was certainly introduced from China, yet the wild form, the original of the garden variety, grows in the south-western parts of Japan. Nowadays a great number of European and American plants are introduced into Japanese gardens, while quantities of Japanese plants are exported to foreign countries and especially to England, where it always gives me the intensest joy to see the plants of my native land.

THE ECOLOGY OF *CALLUNA VULGARIS*.

By M. Cheveley Rayner, B.Sc.,

(Lecturer in Botany, University College, Reading).

[Plate III and Two Text-Figures].

THE Ling (*Calluna vulgaris*) is usually recorded as forming definite heath communities, in competition with other plants, only on poor and often acid soils, such as those which occur on Bagshot sands, or less typically on the washed-out soils sometimes found overlying limestone and chalk.

A somewhat anomalous distribution of *Calluna* on parts of the chalk downs of Berkshire and Wiltshire has been described in a previous communication.[1]

In that paper it was recorded that sporadic communities of this plant occur on the higher parts of the downs, forming patches of typical heath vegetation quite different in character from the so-called "chalk heath" of the South Downs and elsewhere.

The distribution of these communities is roughly determined by the overlying deposits of clay-with-flints, which give rise in this neighbourhood to fertile loamy soils, with a low percentage of calcium carbonate. The soil in question has the appearance of a fertile loam, and the conditions generally give the impression that the heath flora has become established on the more fertile soils of the area, in competition with the surrounding vegetation.

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[1] Rayner, M. C., and Jones, W. N. "Preliminary Observations on the Ecology of *Calluna vulgaris* on the Wiltshire and Berkshire Downs." New Phytologist, Vol. X, 1911, p. 227.

Mechanical and chemical analyses support this view and indicate that the soil monopolized by *Calluna* is in every respect a good fertile loam with a high percentage of available mineral matter (*loc. cit.*, pp. 236, 237).

A low percentage of calcium carbonate excepted, there is no evident factor to account for the successful competition of the heather; the soil reaction is neutral, and the only feature of note chemically is the rather high ratio of magnesia to lime.

With regard to the significance of this ratio as it affects plant growth, there is at present a conflict of opinion and the evidence adduced by different observers is somewhat contradictory.

Two distinct problems were suggested as a result of these observations:—

(i.) The nature of the soil conditions which allows *Calluna* to compete successfully with other plants on small areas of fertile soil.

(ii.) The significance of calcium carbonate as a factor determining the spread of *Calluna* from those sharply defined areas to the surrounding "down" soil.

These problems do not appear to be capable of explanation in terms of current hypotheses, nor do these hypotheses throw clear light on the causes which determine the calcicole and calcifuge habit exhibited in varying degrees by so many plants.

The present investigation was undertaken primarily in order to study the biological significance of the sharp delimitation of *Calluna* under the conditions described, and secondarily, in order to ascertain whether the facts obtained in the course of the investigation might throw light on the larger question of the ecology of calcicole and calcifuge plants in general.

(*a*). Experimental work was begun with two objectives in view. Sand and water cultures were grown in the hope of obtaining evidence as to the effect of alteration in the proportions of lime and magnesia in the culture solutions.

Water culture experiments carried on continuously for twelve months pointed to the conclusion that further work in this direction was premature at this stage of the enquiry and unlikely to lead to definite results. They were therefore discontinued: the results obtained are briefly summarized at the end of this paper.

(*b*). Pot cultures were started using seed and fresh soils from the field, with a view to detailed observations on the behaviour of seeds and seedings under experimental soil conditions. Full analyses of the soils are available and have been recorded in a previous paper (*loc. cit.*). In these analyses the soils are referred to as "heather area" and "soil over chalk" respectively. For the sake of brevity they will be known as "heather" soil and "chalk" soil in the present paper. The former is apparently a good fertile loam although the percentage of calcium carbonate is low: the latter is a typical chalk-down soil containing 41·8% calcium carbonate.

It is convenient to deal with the results of these cultures under two heads:—(A) Germination, (B) Growth.

A. *Germination.* Seed was collected in the capsules during October, dried in the laboratory at air temperature and stored in paper bags. When required it was rubbed down, sieved, and the seed picked out by hand.

The seed is very small, with a rough testa, abundant oily endosperm and a minute straight embryo. Sowings were made in pots of fresh soil, under glass, using approximately the same number of seeds per pot, and records kept of the rate of germination, the number of seedlings, and the growth and condition of the roots and shoots at successive stages.

In the autumn, germination begins 25—30 days after sowing, and is usually rather slow and irregular. In the spring it takes place more uniformly, 16—19 days after sowing.

In "heather" soil, seeds germinate at the same rate and exhibit about the same germination capacity as on blotting paper in a germinator. As compared with this, the rate of germination is greatly retarded and the germination capacity markedly lowered in the "chalk" soil. A majority of the seeds do not germinate. Germination of the remainder is delayed—seedlings first appearing after two or three months and then in very small numbers. Seeds continue to germinate irregularly for six months or longer, but the total germination capacity is extremely low as compared with the controls.

In order to compare the behaviour of *Calluna* seed in this respect with that of other plants, sowings were made, in the two soils, of Foxglove (*Digitalis purpurea*) as a representative calcifuge, and of Kidney Vetch (*Anthyllis vulneraria*) as a calcicole. The latter plant is abundant on the down soil in the field.

In each case germination is simultaneous and the germination capacity similar in the two soils.

The phenomenon of retarded germination in a soil unfavourable to the growth of the plant does not appear, therefore, to be one which occurs generally in the case of calcicole and calcifuge plants.

Heating *Calluna* seed for some hours at a temperature of 67°C. to 70°C. hastens germination, the acceleration so produced being more marked in the autumn.

Seed so treated germinates more evenly and about seven days sooner than unheated seed.

Heating for a longer period, *e.g.*, twenty hours at 70°C. affects the germination capacity adversely, but not the vitality or rate of germination of those seeds which germinate.

No difference can be detected in the behaviour of seeds germinated at once after heating and those kept for several weeks before sowing.

Partial sterilization of the soil, by treatment with vapour of carbon bisulphide and by heat, gives somewhat irregular germination results, which are summarized in Table I. The soil for these experiments was treated as follows:—

Small quantities of soil were spread out in carbon bisulphide vapour for three or four days, then exposed freely to the air for several days, placed in small sterile pots and watered with distilled water, Other samples of soil were subjected to intermittent heating at 92°C. and 98°C. on five successive days, moistening with sterile water between each heating. The seed used for these experiments was in all cases untreated, and control seeds of oat placed in the pots germinated normally.

Reference to the tabulated records shows that the behaviour of the seedlings when the *unfavourable* soil is subjected to partial sterilization is noteworthy and in striking contrast with their reaction to the same soil untreated. The germination capacity remains low as in untreated soil, but the rate of germination is accelerated. The resulting seedlings develop a larger and more normal root system (Plate III, Fig. 1d).

B. *Growth.* Seedlings of *Calluna* are small and slow-growing. The primary root elongates slowly, but soon after germination several adventitious roots grow out in rapid succession from a thickening at the base of the hypocotyl.

The roots are almost transparent and provide beautiful material for observing the details of root structure. Root hairs are absent; the cortex consists of a few cell rows only, and the whole root is extremely slender and delicate.

TABLE I.—GERMINATION OF *CALLUNA* SEED.

			Seedlings First Appear.	Number (Approximate).	Remarks.
Moist Air.	*Autumn.*	1 Control (seed untreated)	28 days	42%	Germination of untreated seed is very irregular in autumn.
		2 Ditto...	26 ,,		
		3 (Seed heated 4 hours at 67°C.)	17 ,,	50%	Germination more uniform. A majority of the seeds germinated simultaneously.
	Spring.	4 Control (seed untreated)	16 ,,	2 Seedlings	In the spring acceleration is less marked, but germination takes place more uniformly in the case of heated seed.
		5 (Seed heated 4 hours at 70°C.)	16 ,,	40%	
Untreated Soil.	*Late Autumn.*	*Heather Soil* (1)	23 days	100 seedlings	Approximately the same number of seeds sown in each case (250-300). In pots 1 and 2 seedlings appeared uniformly in pot, and majority ultimately germinated. In pots 3 and 4, 15-20 seedlings had appeared at the end of 6 months and represented the total germination capacity.
		,, ,, (2)	21 ,,	50 ,,	
		Chalk Soil (3)	68 ,,	5 ,,	
		,, ,, (4)	112 ,,	3 ,,	
Partially Sterilized Soil.	*Heather Soil.*	Control	53 days	Numerous seedlings	Germination extremely slow, possibly owing to spell of very cold damp weather.
		CS_2 Vapour	94 ,,	4 seedlings	Result not confirmed.
		Heated	50 ,,	Numerous	More numerous and rather more vigorous than control.
	Chalk Soil.	Control	112 days	2 seedlings	Total germination capacity not materially affected by either treatment; remains very low.
		CS_2 Vapour	50 ,,	2 ,,	
		Heated	55 ,,	1 ,,	

From the earliest stages, whether growing in moist air or in soil, the roots are infected with an endotrophic mycorhiza. Branched hyphæ project from the surface and many of the cortical cells contain the characteristic "knots" of mycelium.

The plumule is undeveloped in the resting embryo and growth of the shoot is slow, especially in the early stages.

In the "heather" soil seedlings grow normally; the leaves are bright green and a vigorous much-branched root-system is rapidly formed (Plate III, Fig. 1a).

Partial sterilization of this soil by carbon bisulphide, as described above (p. 62), gives an impetus to vegetative growth and the seedlings, for a time, compare favourably with the controls. Examined microscopically the roots of such seedlings are cleaner and fungal infection is rather less conspicuous (Plate III, Fig. 1b).

In the "chalk" soil, growth is practically inhibited.

The few seedlings which germinate remain in the seed-leaf stage for many months. Sometimes no other leaves are formed: those which do appear are small and chlorotic, and the whole shoot usually becomes bright red in colour. Root growth is almost completely checked; many lateral roots begin to develop, but their tips are strongly recurved and often show brownish discoloration (Plate III, Fig. 1c).

Seedlings may remain in this condition for months, making repeated but ineffectual efforts to form an adequate root system: if transplanted to the other soil, they at once recover and grow normally. Examined microscopically, these abnormal roots are remarkable, not only for the retarded growth and peculiar curvatures which they exhibit, but for the association with them of dense colonies of bacteria. The latter are especially conspicuous about the tips, which are usually invested with dense bacterial sheaths.

Bacteria are also abundant in and about many of the cortical cells and around the apices of young emerging lateral roots (Plate III, Fig. 2b, Fig. 3).

In "chalk" soil sterilized by either of the methods described on page 62 root development is more normal for a time. Bacterial growth appears to be retarded; a more normal root system is developed and reddening of the shoot takes place rather more slowly. This improvement, however, is temporary, and eventually the same symptoms appear as in roots in untreated soil (Plate III, Fig. 1d). In all these abnormal roots, mycelium, though present, is scanty in amount, few hyphæ project from the root and they are often crowded with bacteria.

The effect of watering seedlings growing in "heather" soil with a watery extract of "chalk" soil has been tried, with the following results :—

After four months of regular treatment seedlings in small pots do not differ markedly from the controls. After six to seven months treatment, seven out of eight seedlings so treated begin to show signs of injury. Growth was stunted, the foliage yellowish and discoloured, and the leaves dead on some of the older shoots (Plate III, Fig 4).

Examined microscopically, the roots of these seedlings show in a rather less marked degree the same peculiarities as have been already described for roots growing in "chalk" soil. Root growth is evidently checked, the tips show marked curvatures and are often invested with a dense mantle of bacteria. Mycorhizal growth is poorly developed and the general appearance of the roots quite characteristic.

Seedlings growing in larger pots responded to similar treatment much more slowly. After treatment for the same length of time, the growth and general condition of the shoot was practically unaffected.

Many of the root-tips, however, when examined microscopically, showed characteristic association of the mycelium with bacteria, the relations of the hyphæ with the latter being much more evident in such early stages than they are later when the tip has become invested in a dense sheath of bacterial growth.

Other seedlings growing in "chalk" soil were watered with an extract of "heather" soil prepared similarly to that used in the last experiment. This experiment was begun shortly after germination, before the ill effects of the unfavourable soil conditions had become marked, and was continued for six months. At the end of that period the controls—watered with distilled water—were dead ; the seedlings in the three pots under treatment were alive ; the characteristic purpling of the leaves had appeared, but most of the plants had made four to six leaves on the main axis.

The change in the root system was more remarkable and is shown in Plate III, Fig. 5.

As is evident from a comparison of this photograph with that of the seedlings shown in Plate III, Fig. 1c, the root system is many times larger than that of a seedling from untreated soil, During part of the time occupied by the experiment, growth of the roots had apparently been almost normal and resulted in the formation of a more fully developed root system.

Several points of interest are suggested by these observations:

(i). Since the unfavourable and favourable soil conditions respectively can be supplied in a filtered, unboiled soil extract, they are either of a chemical or biological nature.

(ii). If the conditions be biological, and the injurious effect can be produced by supplying an organism present in the unfavourable soil simultaneously with the conditions which favour its growth, all the plants so treated might fairly be expected to behave in the same way.

Unfavourable symptoms appear, however, much more slowly in plants growing in large pots, thereby suggesting that the unfavourable factor is chemical in nature and that as soon as a certain concentration in the soil is reached, an unheathy condition of the roots is induced owing to disturbance of their normal relations with the micro-organisms present,—a view confirmed by the results of the treatment when an extract of "heather" soil is used for watering seedlings growing in "chalk" soil.

Whether the unfavourable effect is a *direct* result of the bacterial colonies which beset the roots, or whether it is *indirect* and due to the effect of these colonies on the micorhizal fungus, remains an open question, as does also the important point as to whether the pathogenic effect of the bacteria is dependent on a change in the chemical condition of the soil, the organism being present in both cases, or whether the latter is peculiar to the soil on chalk.

This experimental work, combined with examination of the roots of large numbers of seedlings grown under different soil conditions, suggests that the relation between the roots of *Calluna* and the micro-flora of the soil in which it is growing is an intimate one; that the balance between these biological factors may be very delicate, and only maintained in equilibrium, *i.e.*, in such relations that the result is either beneficial or indifferent to the plant, under definite soil conditions.

It is only by attacking this larger problem that a clue can be found to the soil conditions which determine growth in any given locality such as the one under consideration, where the soil differs in respect to certain constituents over a small area.

In the case of such plants as *Calluna* and its Ericaceous allies, the relation of the roots to the soil is evidently rendered more complex by the presence of a mycorhizal fungus, of which the full significance to the plant is still in need of demonstration. The details of fungal infection, and the ability of the plant to germinate and grow without its fungal partner have also yet to be described in the case of *Calluna*.

An obligate association of definite races of bacteria with the roots of plants has already been suggested[1], and it would seem not unreasonable to expect that such associations would become much more complex in the case of a plant, the roots of which constantly contain mycorhiza. It is claimed that several species of nitrogen-fixing fungi have been isolated and cultivated from the mycorhiza-bearing roots of various Ericaceous plants, including *Calluna vulgaris*, but absolute demonstration that this was the case could not be made, since the seedlings were never obtained in a sterile condition.[2] Similar relations are suggested far *Vaccinium corymbosum*,[3] and have indeed already been inferred for most plants which form root associations with either fungi or bacteria.

Before the main problem of the relations of the mycorhizal fungus to the plant and of the former to the soil and its bacterial flora can be attacked, it is necessary, therefore, to learn whether the association of the plant with its mycorhizal fungus is an obligate one, and for that purpose to determine the following points :—

(i). At what stage in the life-history of the plant, and from what source, does infection of the roots take place?

(ii). Is it possible (*a*) to germinate, (*b*) to grow *Calluna vulgaris* without infection of the roots under sterile conditions?

Having a knowledge of these facts, it should be possible to infer the existence, or not, of fundamental relations between the plant and special micro-organisms of the soil; to determine if any of the latter are indispensable for its growth, and whether the soil preferences and peculiarities of *Calluna* are directly associated with them, or are specific to the plant, apart from its symbiotic relations with any other organism.

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[1] Gottheil, O. "Botanische Beschreibung einiger Bodenbakterien." Centralbl. f. Bakteriologie, Bd. 7, p. 430.

[2] Ternetz, C. "Ueber die Assimilation des atmosphärischen Stickstoffes durch Pilze." Jahrb. f. wiss. Bot., Bd. 44, 1907, p. 353.

[3] Coville, F. V. "Experiments in Blueberry Culture." U.S. Dept. Agric. Bureau of Plant Industry, Bull. No. 193, 1911.

It has already been mentioned (page 64), that the roots of seedlings when germinated are always infected with mycorhizal fungus.

Microscopic examination of young seedlings, protected against infection from without during germination, shows that emergence of the radicle is accompanied by growth of fungal hyphæ from the testa. Some of these hyphæ grow across to the root and infect the seedling root, most commonly, *via* the cells of the root cap. This mode of infection appears to be very regular and characteristic. Bacteria are also associated with the seed-coat, but these are not conspicuous in seeds germinated under healthy conditions.

Infection of the seed-coat by fungi and bacteria occurs commonly in many seeds, such infection taking place after the seeds have been exposed to the air.[1] In the case of *Calluna* seeds, in addition to this superficial infection, a fungus is present, which is identical morphologically with the mycorhizal fungus present in healthy roots.

So far as could be ascertained from examination of fresh material, endosperm and embryo are free from infection in the resting seed. Microtome sectons of the seed pointed to infection of the testa only, and therefore to the possibility of sterilizing the seeds. The delayed infection observable in heated seeds (page 64) also supported this view, which has now been confirmed as correct, by germinating seedlings in a sterile condition, after adequate sterilization of the seed-coat.

It remains to enquire the source of infection and at what stage of seed development it takes place.

Examination of the ovary of the flower after fertilization reveals the fact that, in common with other parts of the flower the ovary wall is infected with fungal hyphæ.

Infection of the young seed-coat takes place from this source while the seeds are still enclosed in the ovary.

A full account of the details of this infection of the seed-coat, and of the mode of infection of the flower—whether from without at the period of flowering or from within by a more widespread distribution of the mycorhizal fungus in the plant than has been commonly assumed—is reserved for a subsequent paper.

Fungal infection of the testa is difficult to observe in the resting seed, but in favourable cases the presence of hyphæ and more rarely of isolated spores can be demonstrated. The evidence at present available, points to infection of the coat by spores as relatively rare. This may, to some extent, account for the differential results obtained when attempting to sterilize seed. Effective sterilization is doubtless more difficult in the case of seeds, to which spores adhere so closely that they are not dislodged by washing or centrifuging. Attempts to sterilize the seed by immersion in hot water at 70°C., 60°C., and 52°C. respectively for fifteen minutes led to all the seeds being killed by the treatment. Seeds soaked in ·01% corrosive sublimate for five minutes always gave a large proportion of infected seeds when sown.

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[1] Arcichovskij, V. "Ueber die Methoden zur Gewinnung mikroorganismenfreier Samen." Centralb. f. Bakt., Bd. 36, 1912, Nos. 15—18.

The following method was then tried and although sterile seedlings were not obtained, it yielded interesting results in another direction.

Soil extracts of the two soils were prepared, using 25 grams of fresh soil to 300c.c. distilled water; agar, in the proportion of 1·5% was added and the media sterilized in the usual way.

Seed was sterilized by soaking for thirty minutes in ·01% corrosive sublimate, washed repeatedly with sterile water and sown with a sterile pipette in Petri dishes of the above media, which were kept for some days at a temperature of 37°C. At the end of five days the two sets of plates were strikingly different in appearance, this observation applying both to the sterilized cultures and to the controls for which unsterilized seed was used.

The results are summarized in Table II.

TABLE II.—SEED CULTURES IN AGAR SOIL EXTRACTS.
TEMP. 37°C. 5 DAYS.

	SEED TREATED CORR. SUB. ·01%	CONTROL (SEED UNTREATED).
(A) "Heather" Soil Extract.	Many seeds apparently sterile. Some with a zone of mycelium. Plates sterile except in the immediate neighbourhood of seeds.	Majority of the seeds surrounded by a zone of mycelium. A few seeds apparently unaffected.
(B) "Chalk" Soil Extract.	Almost every seed or group of seeds with a zone of bacterial growth. Mycelium almost or entirely absent. Plates otherwise sterile.	Majority of seeds surrounded by bacterial colonies. Mycelium, if present, always accompanied by vigorous bacterial growth.

Since a majority of the seeds in each plate were infected, the Petri-dishes were opened and the growths examined microscopically. In the "chalk" soil cultures, well-defined bacterial colonies were present round all seeds but three, in a total of about one hundred seeds.

Hyphæ were absent from the outer limits of many of these colonies. In others mycelium was present but generally showed attenuated growth and the hyphæ were invested with a sheath of bacteria (Plate III, Fig. 6).

Masses of bacteria occurred in close association with the mycelium, which was rarely present in sufficient amount to alter the macroscopic appearance of the colony.

In the "heather" soil cultures a vigorous zone of mycelium was present around every infected seed. Mycelial growth round "sterilized" seeds was apparently pure but had not reached the sporing stage.[1]

Bacterial colonies, closely resembling those in the "chalk" soil cultures were present in many of the growths. These were not sufficiently prominent in any single case to affect the macroscopic appearance, which was always of a mycelial character.

The close association of bacteria with the hyphæ, which was a striking feature in the other plates, was not observable.

At this stage of development the difference in the two sets of plates was very striking:—

The cultures for which an extract of "heather" soil had been used were practically free from bacterial growth; in those for which an extract of the "chalk" soil was used they were the most prominent feature.

It was the striking contrast presented by this set of plates, in conjunction with the appearances noted in the roots of young seedlings growing in soil cultures, that first suggested the possibility of a biological relation between the mycorhizal fungus and soil bacteria.

It is significant that the mycelium grows vigorously in a medium made up with an extract of the one soil and is practically eliminated by bacterial growth in that made with an extract of the other soil, the seeds in both cases having had precisely similar treatment. The appearance of the hyphæ in the latter case strongly suggests that given certain conditions of nutrition, bacteria, constantly associated with the seed, can multiply and become pathogenic to the fungus which is also present on the seed coat. The same inference is suggested by the behaviour of the mycorhizal hyphæ on the roots in pot cultures of the "chalk" soil.

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[1] A fungus invariably present in these colonies has since then been identified with the species occurring as mycorhiza in the roots.

It is recognised, of course, that these pathogenic relations may be secondary in both cases, and determined by inability of the mycelium to thrive under the conditions supplied. In either case they seem to be pertinent to the inquiry. A large proportion of the seeds in these cultures germinated, and no difference was apparent either in rate of germination or in germination capacity. This difference of behaviour as compared with soil cultures may be due to the position of the seeds on the surface of the media, but requires further investigation. The seedlings grew for a month or more, but soon showed symptoms of starvation in all the cultures, due no doubt to the paucity of food material in the soil extracts.

The next attempt to sterilize seed was successful.

Similar extracts were prepared, made up with agar, sterilized, and placed in sterile Petri dishes. Seeds were soaked for thirty minutes in water, precautions being taken that the seed coats should be thoroughly wetted. They were then immersed for short periods (two minutes or less) in a 1% solution of corrosive sublimate, washed as before in many changes of sterile water and sown, fewer seeds being placed in any one dish. Care was taken to make the conditions as aseptic as possible and the cultures were placed under a bell-glass in a small greenhouse, all the surroundings having previously been washed down with a strong solution of Jeyes' fluid in water.

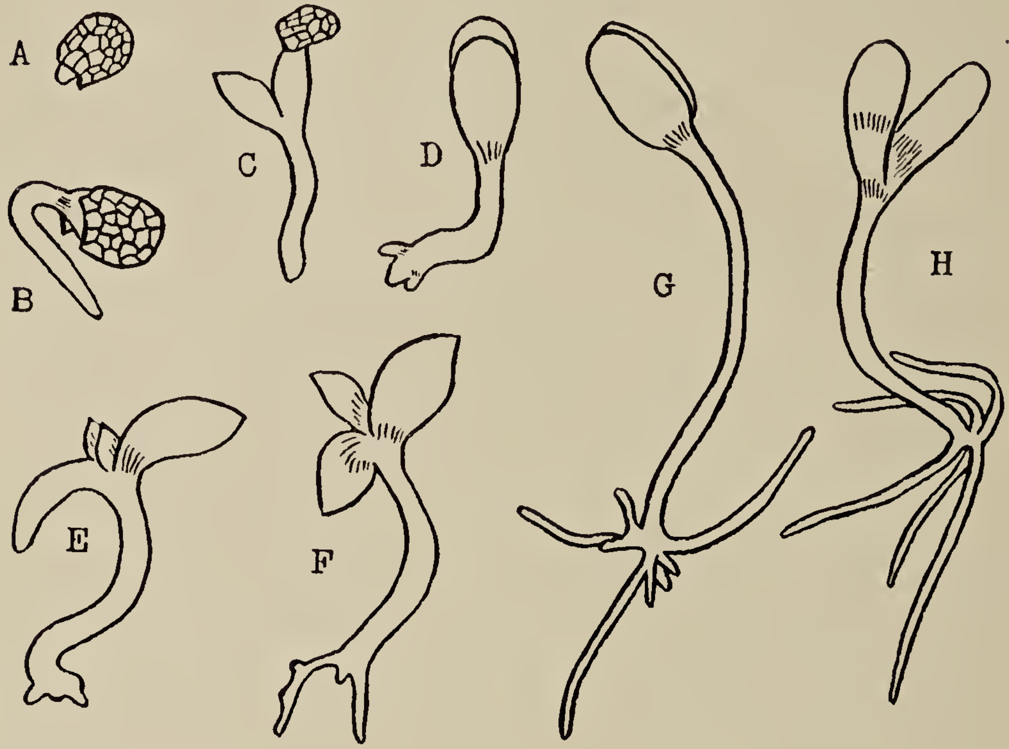
At the end of nineteen days three plates contained each a number of germinating seeds and were absolutely free from micro-organisms.

No trace of fungal or bacterial growth appeared round any of these seeds, about 50% of which germinated at the usual rate.

The early stages of growth of these sterile seedlings are otherwise normal and precisely similar to those of infected seedlings.

The seedlings were transferred singly to special culture tubes fifty-three days after sowing, *i.e.*, about five weeks after germination. Many of them formed several leaves and developed the rudiments of roots while still in the seed dishes (Text-fig. 1, A—F).

The cotyledons and young leaves were green and the seedlings appeared to be perfectly healthy, with the exception that they had made no attempt to send down roots into the culture medium, or to place the axis in a vertical position. For comparison with these sterile seedlings, there are shown, in Text-fig. 1, two seedlings (G, H) germinated in moist air from unsterilized seeds and infected with mycorhiza.



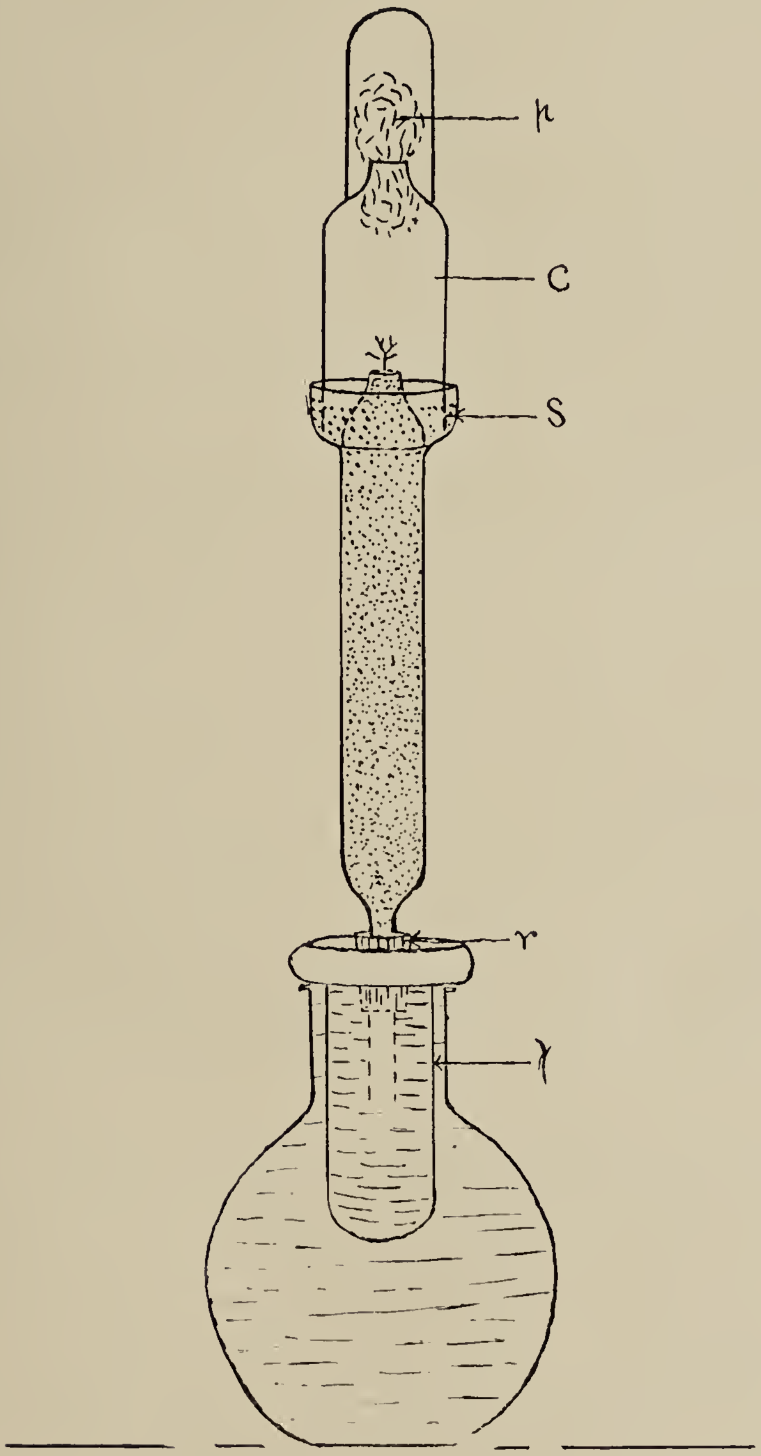
Text-fig. 1. Seedlings of *Calluna vulgaris*. A to F, sterile seedlings germinated under aseptic conditions on agar plates. (A to C, four weeks after sowing; D to F, eight weeks after sowing). G and H, seedlings germinated in moist air, seeds unsterilized, seedlings infected with mycorhiza; eight weeks after sowing. All × 12.

The tube shown in Text-fig. 2 is used for sand cultures; with slight modification similar tubes can be used, without filters, for water or agar cultures. After filling the sterilized tubes with agar media or with fine quartz sand as the case may be, the latter washed and sterilized in the usual way, the whole apparatus is sterilized again and when cool, is ready for planting.

After placing the filters in the solutions, the sand at the surface becomes moist, from capillary rise of the solutions, in about three hours.

The seedlings can be rapidly transferred to the tubes and the covers replaced. By filling the shoulder S with sterilized sand, the tubes can be manipulated without risk of knocking off the covers after sterilizing, and by moistening this sand with sterile water, a moment before the joint is made air-tight with hot paraffin wax, the air inside the cover C is maintained in a moist condition.

Once planted and placed under suitable conditions, little attention is required.



Text-fig. 2. Apparatus for growing sterilized seedlings in sand cultures. Lettering :—*p*, cotton wool plug ; *c*, glass cover ; *s*, shoulder filled with sterile sand ; *r*, rubber cork ; *f*. Massen filter candle.

The evidence available as a result of these cultures points to the conclusion that roots are not formed by the seedlings unless infection with a fungus associated with the seed-coat takes place: and that therefore the relations between the plant and its endotrophic fungal partner is an obligate one, under the conditions supplied, *viz.*, a supply of inorganic salts, in a solution favourable to the healthy growth of unsterilized seedlings.

Since roots are not formed, it is impossible to demonstrate with certainty how far the susceptibility of the roots to particular salts and to the concentration and the reaction of the culture media are specific characters of the plant.

It is proposed to deal more fully with these and similar cultures and with the effects of inoculation from a pure culture of the fungus in a subsequent paper.

The evidence is conclusive that the resting embryo of *Calluna* is uninfected; also that, by effective sterilization of the seed-coat, seedlings can be germinated in a sterile condition and can be maintained alive under aseptic conditions for six months or longer. Infection of the plant by the fungus takes place under normal conditions immediately after germination and it is believed that a functional root-system is not formed by the seedling unless such infection occurs.

Hence, the nutrition of *Calluna* is bound up with that of its mycorhizal fungus: and the soil preferences of the plant and the soil conditions which limit its growth are determined *indirectly*, by the ability of the fungus to flourish under the conditions supplied.

In short, the maintenance of a definite biologic relation between the roots and the fungus which infects them acts as a limiting factor to the spread of the plant.

The refusal of *Calluna* to grow in the calcareous soil investigated, and presumably in similar soils elsewhere, is due to a disturbance of these conditions. On this view, the habit usually described as "calcifuge" may be, in this case, characteristic of the fungus rather than of the plant.

Directly connected with this disturbance is the presence of colonies of bacteria closely associated with the roots, especially with the regions where the fungus is usually prominent.

It is suggested that the bacteria are to be regarded either as pathogenic agents, or as indicators of soil conditions unfavourable to the fungus and therefore ultimately to the plant.

There is no doubt that the abnormal growth exhibited by the roots in unfavourable soil is directly correlated with the presence of an investing sheath of bacteria on these roots, but the evidence is not conclusive that the organism concerned is the inducing cause of the unhealthy condition.

SUMMARY.

1. As shown in a previous communication, small and sharply defined communities of *Calluna vulgaris* occur on the Wiltshire and Berkshire Downs, associated with soils on clay-with-flints.

The distribution of these heather communities is anomalous, in that they have monopolized areas of fertile soil.

Experimental work was undertaken to investigate the nature of the factors which limit the spread of *Calluna* from these areas to the surrounding down soils and indirectly to throw light on the significance of the calcifuge habit as shown by the soil relations of *Calluna* and its allies.

2. As demonstrated by pot cultures in soil from (*a*) a heather area, (*b*) soil overlying chalk, *Calluna vulgaris* grows *normally* in the former, *abnormally* in the latter.

3. Abnormality of growth is exhibited in (*a*) reduced germination capacity, (*b*) retarded germination, (*c*) arrest of root and curvatures of growing region, (*d*) arrest of shoot, (*e*) small size and red colouration of leaves.

4. Intimately connected with these abnormalities is the presence of colonies of bacteria on the roots, especially around the tip, and also a marked diminution of vigour in the growth of the mycorhizal fungus.

5. The abnormalities of growth can be *induced* in seedlings growing in "heather" soil by watering with filtered extracts of the unfavourable soil, if the treatment is continued over a considerable period. The unfavourable factors are presumably of a chemical nature.

6. The result of germinating unsterilized or imperfectly sterilized seeds in agar media, made up with extracts of the two soils named, shows that the development of the fungal and bacterial elements of the micro-flora associated with the seed-coat is determined *qualitatively* by the nature of the soil extract used.

With an extract of the heather soil, the mycelial constituent is predominant; with an extract of the down soil, colonies of bacteria constitute the prominent feature of the growths associated with the seed-coat.

7. Seedlings of *Calluna vulgaris* are infected by the mycorhizal fungus immediately after germination.

Infection of the primary root takes place by a growth of mycelium from the seed-coat, the latter being infected while still in ovary.

8. The resting embryo and endosperm are free from infection.

9. The fungus isolated from the seed-coat is morphologically identical with one obtained in agar cultures of pieces of healthy root.

10. Seeds can be sterilized and seedlings germinated in a sterile condition, *i.e.*, free from fungal or bacterial infection.

The germination and *early* stages of growth of such sterile seedlings are normal, but in the absence of infection complete arrest of root-formation occurs.

11. The evidence at present available points to the conclusion that the relation between *Calluna* and its mycorhizal fungus is an obligate one, and that successful growth of the plant is ultimately bound up with infection of the roots at an early stage by the fungus, and with the subsequent healthy growth of the latter; hence, the soil preferences exhibited by the plant depend on the maintenance of a biological balance between the roots and the constituents of the microflora which beset them.

12. On this view, the inability of *Calluna* to flourish in the soil investigated is due to a disturbance of the relations maintained under favourable soil conditions between the roots of the plant and its mycorhizal fungus.

The bacterial colonies associated with the roots, more especially with the regions where the fungus is usually prominent, are to be regarded either as pathogenic agents, or as indicators of soil conditions unfavourable to the fungus. The evidence available points to the bacterial colonies as directly correlated with the abnormal growth displayed by the roots, but is not at present *conclusive* that they are the immediate cause of that condition.

13. Water cultures of *Calluna* have not up to the present thrown any light on the significance or not of the relatively high ratio of MgO to CaO in the soil in the area investigated.

They confirm previous observations as to the inability of the plant to thrive in any but very weak solutions.

DESCRIPTION OF THE PHOTOGRAPHS ON PLATE III, ILLUSTRATING MISS RAYNER'S PAPER ON "THE ECOLOGY OF *CALLUNA VULGARIS*."

Fig. 1a. *Calluna* seedlings from "heather" soil, showing normal root and shoot development; six months old.

Fig. 1b. *Calluna* seedlings from "heather" soil treated with carbon bisulphide vapour; six months old. The more vigorous growth as compared with Fig. 1a is less marked than at an earlier stage.

Fig. 1c. *Calluna* seedlings from "chalk" soil, showing arrest of root and shoot development; six months old.

Fig. 1d. *Calluna* seedlings from "chalk" soil treated with carbon bisulphide vapour; six months old. As compared with Fig 1c, root development is more normal.

Fig. 2a. Apex of a young *Calluna* root from "heather" soil, showing normal conditions.

Fig. 2b. Apex of *Calluna* root of same age from "chalk" soil, showing abnormal condition with bacterial investment.

Fig. 3. Part of root apex shown in Fig. 2b, more highly magnified, to show bacteria in sheath.

Fig. 4a. *Calluna* seedling in "heather" soil watered for six months with an extract of "chalk" soil.

Fig. 4b. Control—similar seedling watered during the same period with distilled water.

Fig. 5. *Calluna* seedling from "chalk" soil, watered for six months with an extract of "heather" soil. Control seedlings in similar soil watered with distilled water all died before the end of the experiment. Fig. 1c shows surviving seedlings of the same age in this soil from another series of experiments.

Fig. 6. Mycelium from fungal colonies surrounding seeds, in agar cultures of "chalk" soil, to show investing sheath of bacteria.

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

(Continued from p. 36).

IV.—Relation of Green Algæ to Chlamydomonads.

THERE appears to be strong support for the view that the majority of the Green Algæ may be derived from Flagellate ancestors with two or more equal flagella. In 1897, Chodat (24) pointed out that in the life-history of the lower Green Algæ there may be distinguished three conditions, either of which may become dominant, the other two being then transient or suppressed: (i.) the zoospore condition or motile stage; (ii.) the sporangium condition or unicellular motionless stage; (iii.) the palmelloid condition, in which non-motile cells are connected into aggregates by cell-walls at right angles to each other. In 1900, Blackman (6) published an important paper on the phylogeny of the Algæ, containing not merely a critical summary of modern work bearing upon the problem, but also various far-reaching suggestions as to the lines along which the evolution of the different Algal groups may be traced from Flagellata. Blackman pointed out that among the simple Green Algæ which constitute the group of Protococcoideæ three divergent vegetative tendencies are observed: (i.) a Volvocine tendency towards the aggregation of motile vegetative cells into gradually larger and more specialised motile cœnobia; (ii.) a Tetrasporine tendency towards the formation of aggregations by the juxtaposition of the products of septate vegetative cell-division to form non-motile organisms of increasing definiteness and solidarity; (iii.) an Endosphærine tendency towards the reduction of vegetative division and septate cell-formation to a minimum. The simplest forms showing any one of these tendencies seem clearly to diverge from species of the genus *Chlamydomonas*, which may be regarded as the phylogenetic starting-point of the various lines of Green Algal descent. The line arising from the Volvocine tendency leads to the Volvocales and culminates in *Volvox;* the outcome of the Endosphærine tendency is seen in the Siphoneæ; while the Tetrasporine line has given rise to the great majority of the Green Algæ and through these to the Archegoniatæ and other higher plants.

The phylogeny of the Conjugatæ, Œdogoniales, and a few other isolated groups of filamentous Green Algæ remains in some doubt, owing to the absence of undoubted transitional forms connecting these groups with either the Tetrasporine line on one hand or with distinct Flagellate ancestors on the other. For further details regarding the phylogeny of the Green Algæ, reference should be made to the paper by Blackman already mentioned (6), and to the classification based by Blackman and Tansley (7) upon the principles set forth in that paper; also to the systematic works on Algæ by Oltmanns (95), West (146), and Lotsy (89), in which due prominence is given to modern views of Algal phylogeny. More recently, Fritsch (46) has published a valuable paper, in which is included a useful bibliography; while Pavillard (114) has contributed a resumé of some modern work on Vegetable Protistology—though his "revue rapide" omits entirely the Brown Flagellata and lower Brown Algæ, on which some remarkably interesting work has been published during the last few years.

The relationships of the three lines of Flagellate-Algal descent here suggested are indicated in the accompanying Table A, a fuller explanation of which will be given later.

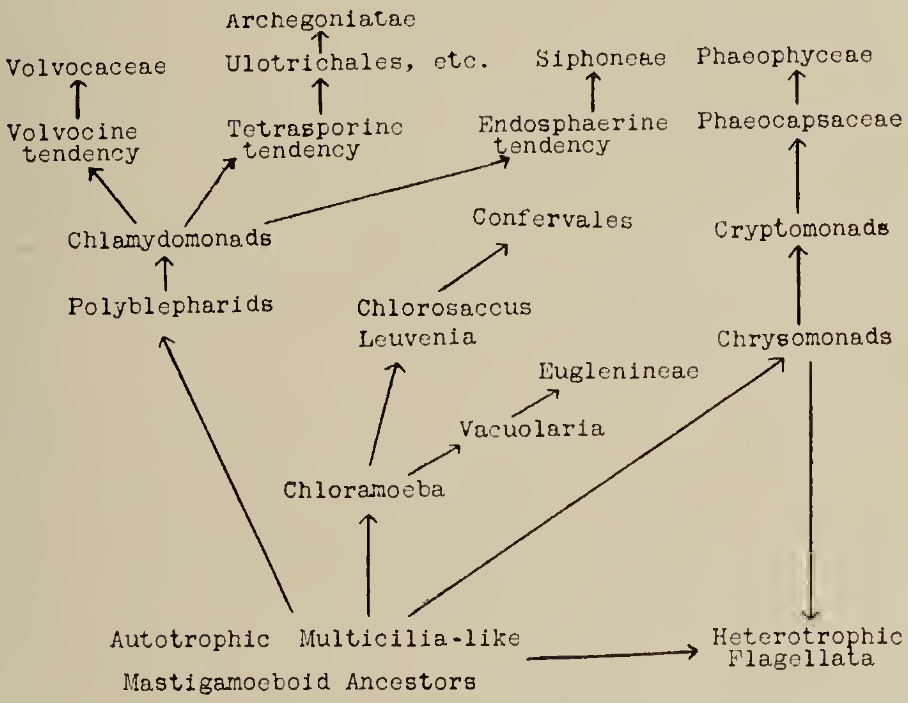


Table A.—Suggested Phylogeny of (I) the Polyblepharid and Chlamydomonad, (II) the Chloromonad, and (III) the Chrysomonad and Cryptomonad lines. For details see text.

Since 1900, perhaps the greatest advances in the study of those Flagellates which are more obviously important in connexion with the phylogeny of the Algæ have been made among the Chrysomonads and Cryptomonads, but before dealing with these we may consider some interesting additions to our knowledge of the group of Green Algæ whose evolution from the Flagellata has, on the whole, been most completely worked out—namely, the Volvocales, using this name to include the entire series of organisms (the "Phytoflagellata" of various zoological writers) representing the transition from Flagellate ancestors to the motile unicellular Green Algæ (Chlamydomonads) and the outcome of the Volvocine tendency which leads to the formation of increasingly complex motile cœnobia and culminates in *Volvox.*

V.—VOLVOCALES.

The Polyblepharidaceæ are included in the Volvocales by Blackman and Tansley (7), Wille (150), and various other writers, though Fritsch (46) regards them as still belonging to the Flagellata, but it appears quite immaterial how this family is placed in a formal scheme of classification, so long as it is recognised that no sharp line of division separates the Flagellata from the lower Algæ and that this remarkable transitional family shows an extraordinarily even balance between the two groups. The Polyblepharids agree with typical Flagellates in being devoid of a definite cellulose wall and in undergoing longitudinal division in the motile phase—but it should be noted that in several genera of Volvocales (*Chlorogonium*, *Brachiomonas*, and even colonial genera like *Gonium* and the oogamous *Eudorina*) division may occur while the flagella are still motile. The Polyblepharids have the characteristic basin-shaped Volvocine chromatophore and a pyrenoid, but—as will appear later—the Cryptomonads and some of the other Chrysomonadineæ would have as much right to a position among the Algæ as have the Polyblepharids if the possession of Algal chromatophores, pyrenoids, starch, and a firm periplast allowing of only slight changes of shape be taken as definitely Algal characters; while, on the other hand, the fact that sexual reproduction occurs in a Polyblepharid *(Dunaliella)* cannot now be regarded as an argument against the reference of this family to Flagellata rather than to Algæ.

Probably the most primitive genus of Polyblepharidaceæ is *Polyblepharis* (Fig. 2, A), in which the broader anterior end of the conical body bears from six to eight flagella in a tuft; in *Pyramimonas* (Griffiths, 52; Fig. 2, B, C) there are four flagella arising from a depression at this end, which is four-lobed, as is also the chromatophore; in *Chloraster* (Fig. 2, D) there is a central fifth flagellum; while in *Tetratoma*, a somewhat doubtful and incompletely known form, there are four flagella inserted at separate points on the anterior half of the spherical body. The genus *Dunaliella* (Fig. 2, E to L), recently described by Hamburger (53) and by Teodoresco (140, 141), evidently forms a transition from the Polyblepharidaceæ to the Chlamydomonads, since it has only two flagella and shows conjugation of isogamous zoogametes; while *Stephanoptera*, recently discovered by Dangeard (35), resembles *Pyramimonas* in structure but has only two flagella, thus connecting *Pyramimonas* with *Dunaliella*—according to Dangeard, the life-cycle of *Stephanoptera* ends in encystment, the cyst having sometimes two nuclei instead of one, but the fate of the cyst was not determined. To the Polyblepharidaceæ probably also belongs the genus *Chlorodendron* (Fig. 2, M to B), placed by Oltmanns (95) in a special family (Chlorodendraceæ), with the closely related, or perhaps congeneric, forms *Prasinocladus lubricus* Kuckuck and *Englenopsis subsalsa* Davis—these have recently been investigated by Dangeard (34, 36) who regards these forms as being closely related to the Carteriaceæ (see below). In the Chlorodendreæ, branching colonies are produced by the localised secretion of mucilage derived from the periplast, or cell-wall, of the dividing cells, and this family, or sub-family, forms an interesting side-line of colonial development arising from a *Pyramimonas*-like type.

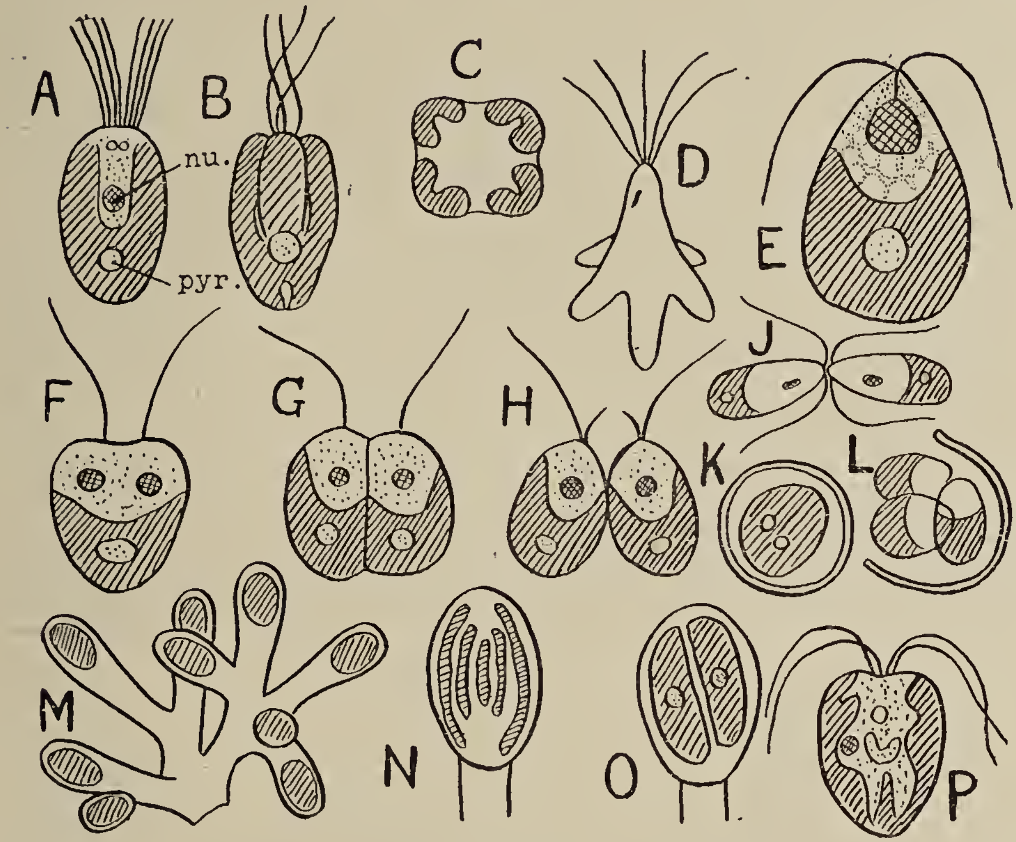


Fig. 2. POLYBLEPHARIDACEÆ.—A, *Polyblepharis singularis* Dang. B, C, *Pyramimonas delicatulus* Griffiths: C, anterior view showing extremities of lobes of chromatophore. D, *Chloraster gyrans* Ehrb., showing stigma or "eye spot." E to L, *Dunaliella salina* (Dun.) Teodor.: E, vegetative cell, with bell-shaped chromatophore, large nucleus, and reticulate protoplasm; F, G, H, stages in division; J, conjugation of zoogametes; K, zygospore; L, rupture of zygospore to set free the zoospores. M to P, *Chlorodendron lubricum* (Kuck.) Senn: M, a portion of a colony; N, a single cell of same; O, division of cell; P, motile cell or zoogonidium. A from Dangeard; B, C, from Griffiths; D, from Stein; E and J, from Hamburger; F, G, H, K, L, from Teodoresco; M to P, from Kuckuck.

In setting forth a new classification of the Volvocales, Pascher (108) has adopted the suggestions made by Oltmanns as to the affinities between *Carteria* and *Spondylomorum*, and by Schmidle as to those between *Sphærella* and *Stephanosphæra*, and has separated these genera from the remaining Volvocales, dividing this order into the four families, Polyblepharidaceæ, Carteriaceæ, Sphærellaceæ, and Chlamydomonadaceæ. Wollenweber (153) has suggested that the Volvocine line shows progressive reduction in the number of flagella and of contractile vacuoles, hence *Carteria* and *Sphærella* may be regarded as more primitive than the Chlamydomonads, the former in having four flagella and the latter in having numerous contractile vacuoles (as many as sixty in *S. Drœbakensis*). It is, however, rather difficult to determine just which cytological characters should be regarded as relatively primitive and which as relatively advanced among the Volvocales. For instance, numerous contractile vacuoles are found not only in *Sphærella* but also in *Chlorogonium* (which differs from the Polyblepharids and most of the simpler Chlamydomonads in showing transverse instead of longitudinal division), and in *Agloë*, a form with somewhat specialized cell structure. *Carteria* and *Spondylomorum* agree in having four flagella and in other characters, but though *Carteria* is usually stated to have a pyrenoid, Jacobsen (61) has described a species (*C. ovata*) which has none; according to this writer, *Spondylomorum* is also without a pyrenoid; while *Chloromonas* is distinguished from its ally *Chlamydomonas* solely on the ground that it lacks a pyrenoid, but this simply means that systematists have described pyrenoidless species or even varieties (Serbinow, 137) of *Chlamydomonas* as belonging to a distinct genus—on other grounds, there is little doubt that *Chlamydomonas* and *Chloromonas* are quite unnatural genera, and will probably have to be revised and split up as the result of further investigations. Most of the Volvocales have a single pyrenoid, but in *Chlamydomonas inhærens* (Bachmann, 3) two or three of these bodies may be present, while in *C. coccifera* (Goroschankin, 51, iii) there are five to eight pyrenoids; two occur in *Sphærella Drœbakensis* and in *Stephanosphæra*, while *Sphærella pluvialis*, *Chlorogonium*, and *Pleodorina* have a large number of pyrenoids.

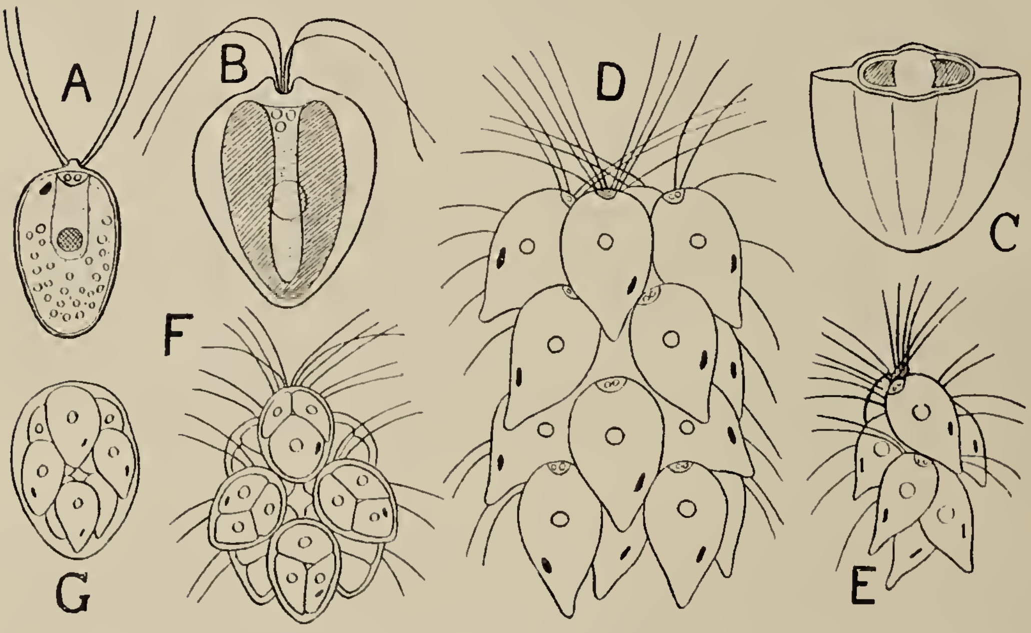


Fig. 3. CARTERIACEÆ.—A, *Carteria ovata* Jacobsen: this species has no pyrenoid, the chromatophore contains numerous small starch grains. B, C, *Scherffelia phacus* Pascher: C shows the cell cut across, to make clearer the wing-like expansion of the cell-wall and the structure of the U-shaped chromatophore. D to G, *Spondylomorum quaternarium* Ehrb.: D, a normal sixteen-celled cœnobium; E, an eight-celled cœnobium; F, division of each cell to form a daughter cœnobium; G, daughter cœnobium not yet set free from mother-cell. A, D to G, from Jacobsen; B, C, from Pascher.

The family Carteriaceæ includes *Carteria* (Fig. 3, A), which has a very thin wall; *Scherffelia* (Fig. 3, B, C), in which the cell is flattened, oval in outline and slightly biconvex in cross-section, with a thick wall which in one species is produced into a marginal wing on either side, two chloroplasts which may or may not be united behind to form a U-shaped structure (obviously derived from splitting of an originally basin-shaped chromatophore), and no pyrenoid; *Tetrablepharis*, a colourless saprophytic form probably derived from *Carteria*; and *Spondylomorum* (Fig. 3, D to G), a colonial form constructed on a plan quite different from that seen in the cœnobial Chlamydomonadaceæ and consisting of sixteen *Carteria*-like cells in four alternating tiers of four cells each, attached to a gelatinous rod-like axis. Among the Carteriaceæ, sexual reproduction is only known in one or two species of *Carteria* which produce isogamous zoogametes. It is of interest to note that the symbiotic "Zoochlorella" found in the Planarian worm *Convoluta roscoffensis* (Keeble and Gamble, 65) is a species of *Carteria*; the single species of *Spondylomorum* (*S. quaternarium*), hitherto known only from Europe and Asia, has recently been discovered by Campbell (20) in California.

Apart from the Polyblepharidaceæ and Carteriaceæ, the Volvocales have a pair of flagella, though a single flagellum occurs in a species of *Polytoma* (Pascher, 108) and in the genus *Mastigosphæra*. The Sphærellaceæ, including the unicellular *Sphærella* (*Hæmatococcus*) and the colonial *Stephanosphæra*, are distinguished from the remaining Volvocales—the Chlamydomonadaceæ—mainly by the peculiar structure of the cell-wall. Various contributions to the knowledge of *Sphærella* have recently been made, especially by Peebles (110), Reichenow (113), and Wollenweber (145, 146). What has usually been taken for a thin outstanding cell-wall is in reality a firm outer layer, while the supposed sap-containing space between wall and protoplast is a thick inner gelatinous coat, traversed by fine branching pits into which protoplasmic threads extend. Reichenow has minutely studied the structure and mitotic division of the nucleus and the shifting of the originally longitudinal axis of division into an oblique or transverse position. The chloroplast is a spongy and reticulate structure, and in *S. pluvialis* there are numerous pyrenoids at the nodes of the network. Though *Sphærella* has been so much worked at, Miss Peebles appears to have been the first to observe a sexual process in this genus; she states that when dry encysted cells of *S. pluvialis* are moistened and exposed to strong light, the contents of the cyst divide into eight to sixty-four gametes which fuse in pairs, as is also the case in *Stephanosphæra*.

(*To be continued*).

[Note.—In the first instalment of this article (January number), certain alterations inserted at the last moment resulted in misprints. On p. 28, "former" (line 7) should, of course, be "formal"; on p. 32, line 3 from bottom, for "form" read "forms"; on p. 33, top line, for "Crystoflagellata" read "Cystoflagellata," and in line 5 from top "hetetrotrophic" should be "heterotrophic." On p. 33, line 18 from top, the substitution of a note of interrogation (?) for a semicolon (;) may be regarded as a piece of unconscious humour—though the reader may, like the author, feel inclined to mark *each* of these "main lines" with a query!]

REVIEW,

"Herbals: their Origin and Evolution. A Chapter in the History of Botany, 1470—1670." By Dr. Agnes Arber. Cambridge Univ. Press, 1912.

No other epoch in the development of Botany has the peculiar fascination possessed by that which elapsed between the renascence of interest in the subject and its firm establishment as a pure science. Botanists are extremely fortunate in having in Dr. Arber a writer who combines a thorough knowledge of the recent growth of the science with an affectionate interest in its childhood and an unrivalled acquaintance with its juvenilia. To these qualifications she adds the other not less important one of literary ability, so, that in a book positively loaded with erudition there is no indigestible page: indeed no page in which one may not find some some happy phrase or quaint quotation.

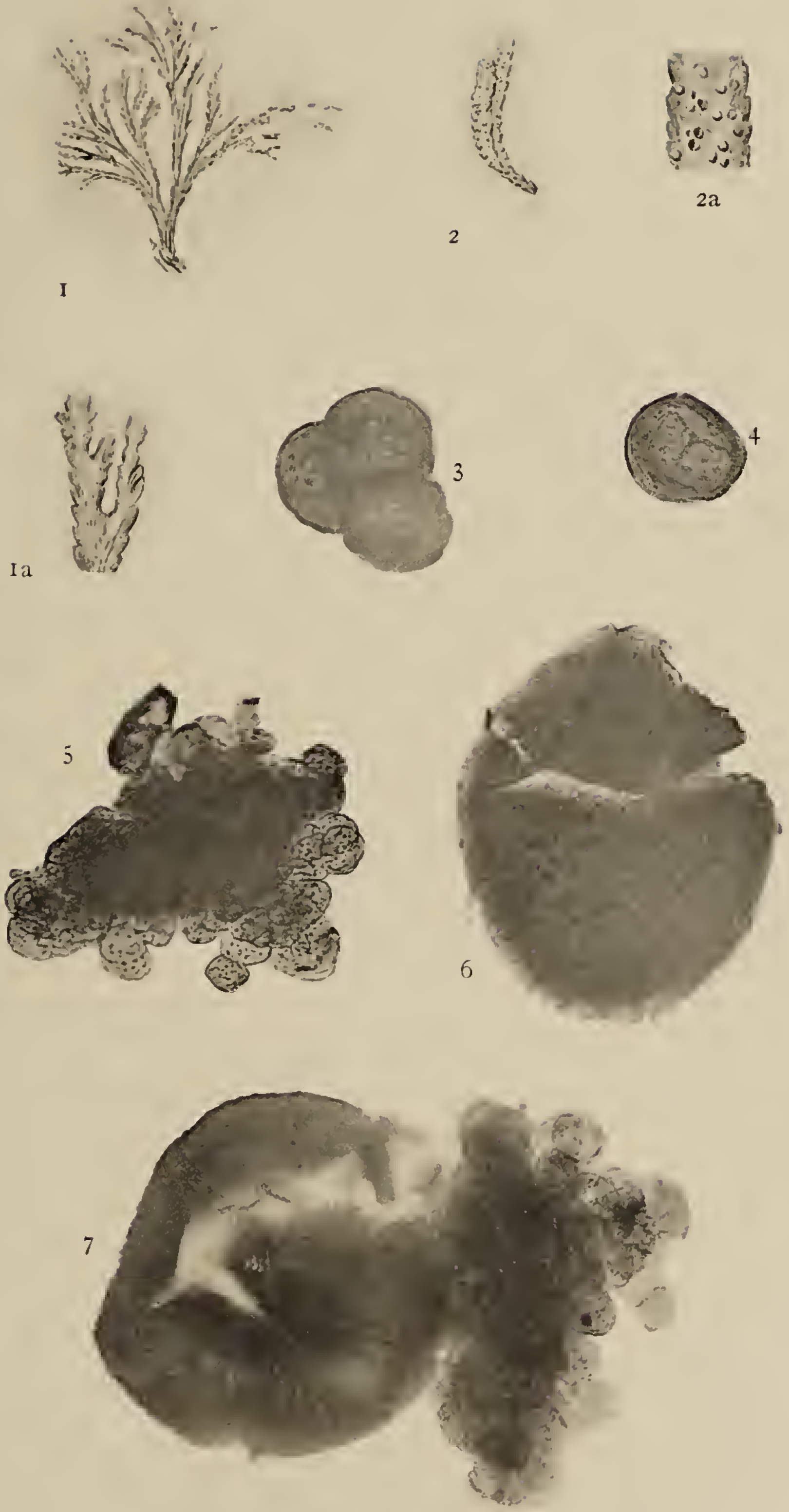
The book opens with a consideration of the earliest known records of observations of plants, those of Aristotle, Theophrastus, the elder Pliny, Dioscorides and Albertus Magnus, although these authors lived earlier than the XV century: their work, especially that of Dioscorides, having such a fundamental importance in relation to the mediæval botany of the Renaissance. The primitive Herbals of the end of the XV century, with their crude, but singularly attractive illustrations, are next considered. A special chapter is devoted to the earliest examples of herbals in England; and here, as in the other sections dealing with works in English, Dr. Arber exhibits to the full her aptitude in the selection of charming passages for quotation.

The next chapter is the most extensive in the book, and deals with the history of the herbal in Germany, the low Countries, Italy, Switzerland, France and England respectively. This is probably the best arrangement of the mass of available material: but it is remarkable to note the internationalism of botanical studies even in those early days. Here we find ourselves among Bock and Brunfels, Fuchs and Camerarius, and witness the culmination of the art of plant portraiture.

Chapter V is devoted to the methods adopted in plant description, and Chapter VII to the evolution of botanical illustration. The latter is admirably full, dealing concisely with the characteristics of the work of the various artists and the development of the power of scientific observation reflected therein: the text being lavishly adorned with well chosen figures reproduced through the skill of Mr. W. Tams.

Of great interest to systematists is Chapter VI on early methods of classification: while the curious will find in Chapter VIII an account of the singular entanglement of botany with astrology; and of the doctrine of signatures, the climax of the anthropocentric notions which have so recently disappeared from orthodox science.

The volume closes with a list of herbals published between 1470 and 1760, a bibliography and a full index. It well printed and bound, and singularly free from misprints. By reason of its varied virtues it will appeal to a wide circle of readers, and will keep alive many valuable things upon which in the lapse of time "oblivion blindly scattereth her poppy." R.H.C.



London Stereoscopic Co. imp.

SELAGINELLITES DAWSONI sp. nov.

SEWARD—A BRITISH FOSSIL SELAGINELLA.

THE
NEW PHYTOLOGIST.

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A BRITISH FOSSIL *SELAGINELLA*.

BY A. C. SEWARD, F.R.S.

[WITH PLATE IV].

THE fact that the genus *Selaginella* is now represented by a single species in the British Flora adds interest to the discovery of a Wealden species differing in habit from the recent type. Palæobotanical literature contains numerous records of herbaceous Lycopods, referred to *Lycopodites*, *Selaginites*, *Lycopodium*, or *Selaginella*, but it is only in a very few cases that the untrustworthy eivdence supplied by a superficial resemblance of the impressions in habit and leaf-form to recent species is confirmed by the discovery of spores.[1] It is almost impossible in many cases to distinguish fossil vegetative shoots of lycopodiaceous plants from those of certain Conifers and Bryophytes or even from some types of Dicotyledons, In the absence of sporangia or spores or of clear evidence of dimorphic foliage the identification of small fossil impressions as species of *Lycopodites* or *Selaginites* seldom rests on a satisfactory basis.

The old generic name *Selaginites* has frequently been applied to fossils which afford no evidence of a closer relationship to *Selaginella* than to *Lycopodium*. In order to avoid the danger of a *suggestio falsi* associated with the use of a name clearly implying affinity to the recent genus, Zeiller[2] instituted the designation *Selaginellites* for fossil herbaceous lycopods which possess two kinds of spores, Brongniart's genus *Lycopodites* being conveniently retained for isosporous types or for such sterile specimens as may with reasonable certainty be regarded as generically identified either with *Lycopodium* or *Selaginella*. Although the great majority of existing Selaginellas differ from *Lycopodium* in the possession of two sizes of foliage leaves, there are some members of the former genus, e.g., the British species *S. spinosa*, which bear leaves of one type only.

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[1] For a general account of fossil herbaceous lycopods, sec Seward (10), pp. 73-91.

[2] Zeiller (06), p. 140.

Selaginellites Dawsoni sp. nov. Plate IV. 1894. Planta incertæ sedis, Seward, Wealden Flora, Pt. I, p. 20, Pl. I, figs. 8, 9.

The specimens on which this species is founded were obtained by the late Mr. Rufford of Hastings from the Fairlight Clay, at the base of the Wealden series at Ecclesbourne on the Sussex coast. I have called this Wealden species *Selaginellites Dawsoni* after Mr. Charles Dawson of Lewes, to whose enthusiasm and generosity the British Museum is indebted for many specimens of plants from the Sussex coast.

In the first volume of the Catalogue of Wealden plants in the British Museum a small branched shoot, agreeing closely with that shown in Fig.1, was described under the non-committal title "Planta incertæ sedis" but, at the suggestion of Mr. Carruthers, it was compared with the slender spore-bearing branches of species of *Lycopodium* included in the *L. Phlegmaria* section.[1] Attention was also called to its resemblance to Conifer shoots of the type frequently referred, without any satisfactory evidence, to such genera as *Widdringtonites* or *Glyptostrobus*.

While recently engaged in the description of Wealden plants[2] acquired by the British Museum since the publication of the second volume of the Wealden Catalogue, I found the specimens represented in Figs. 1 and 2, both preserved on one piece of ironstone from Ecclesbourne but not actually in contact. The smaller fossil shown in Fig. 2 consists of portions of two axes approximately 2 mm. broad, with indistinct impressions at the edges of small crowded leaves and bearing several spherical sporangia 0.3 mm. in diameter on the surface (Fig. 2a). On treatment with nitric acid and potassium chlorate, a method recently described by Mr. Thomas in this Journal,[3] the sporangial walls were dissolved without revealing any microscopical features but numerous microspores and a few megaspores were obtained (Figs. 3 to 7). The microspores tended to adhere together in masses (Fig. 5) and not infrequently in compact tetrads (Fig. 3), the fourth spore in each tetrad being clearly distinguished on focussing. The microspores are approximately 0.04 mm. in diameter and are characterised by a finely tuberculate or pebbled[1] outer coat which gives them a pitted appearance, the depressions between the short rounded tubercles giving the impression of small circular pits (Figs. 4, 5). The three-rayed marking is very distinct on the wall of the spore reproduced in Fig. 4. The megaspores, 0.30-0.35 mm. in diameter, are usually oval or almost spherical with a three-sided pyramidal apex. As seen in Fig. 6, which represents the greater part of one spore with a portion of a second in close association, the thick wall has an irregularly reticulate surface precisely as in the megaspores of several recent species.[2] Fig. 7 illustrates the difference in size between the two kinds of spore and shows the wall of the megaspore opening along the three-rayed apical ridge. In the interior of one of the megaspores a thin inner membrane was noticed, separated a short distance from the much thicker outer wall, presenting an appearance very similar to that in recent megaspores where the exine and intine are often widely separated.[3]

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[1] Seward (94), p. 20, Pl. i, figs. 8, 9. (Rufford Coll., British Museum, No. V. 2328), The specimen reproduced on Plate IV, also from the Rufford Collection, is No. V. 3151.

[2] A short account of *Selaginellites Dawsoni*, without illustrations, is included in the account of these recently acquired Wealden plants communicated to the Geological Society of London.

[3] Thomas ('12).

The very close resemblance, which it may fairly be said amounts to identity, between the basal narrower portion of the fertile fragment shown in Fig. 2 and the vegetative shoot reproduced in Fig. 1 leaves no doubt as to the connexion between these two closely associated specimens. The sterile tufted shoot (Fig. 1), which is undoubtedly specifically identical with that reproduced in the Wealden Catalogue, shows on slight magnification the impressions of small broadly triangular leaves, the tips of which are indicated at the edges of the enlarged portion shown in Fig. 1a. The preservation does not admit of any definite statement as to the occurrence of one or two forms of foliage-leaves.

While it is clearly impossible to speak with confidence as to the precise relationship of the Wealden plant to existing species, there are certain recent types to which it exhibits a very close resemblance, particularly *Selaginella rupestris* Spring. In its densely tufted habit, small leaves, and slender branches this " most widely-spread species of the genus ",[4] which does not occur in Europe, is strictly similar to the fossil form. The agreement presented by the vegetative shoot extends to the spores: the microspores, 0.45 mm. in diameter, have a finely reticulate or pitted exine, and the megaspores, 0.4 mm. in diameter, are characterised by the same kind of reticulate sculpturing as is faintly shown in Fig. 6. Amongst other recent species of similar habit are *S. borealis* Spring, from East Siberia, the Eastern Himalayas, and other regions; *S. involvens* Spring, a Far Eastern type; and *S. cuspidata* Link from Mexico, Cuba, and Central America.

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[1] Lyon ('01): the expressive term pebbled is used in describing the exine of the microspores of *Selaginella apus*, which agree closely with those of *Selaginellites Dawsoni*.

[2] For good figures of recent spores, see Hieronymus ('02). Some megaspores of species of *Selaginella* are figured also by Bennie and Kidston (88), Pl. vi, figs. 22-24.

[3] Fitting ('00), Pl. vi, fig. 23; Heinsen (94), Pl. xvi, figs. 5-7.

[4] Baker ('87), p. 35.

The spores of several recent species are almost identical both in size and surface-features with those of the fossil: the microspores of *S. serpens* and *S. canaliculata* are respectively 0.03 and 0.04 mm. in diameter; the reticulate spores of *S. Martensii* are 0.03 mm. (microspores) and 0.35-0.40 mm. (megaspores) in diameter. In some recent species the spores are larger: in *S. emiliana* the microspores have a diameter of 0.07 mm., while the megaspores exceed 1 mm.

In the Upper Carboniferous species *Selaginellites primævus* (Gold.) and *S. elongatus* (Gold.)[1] the megaspores, the only spores so far discovered, are respectively 0.4-0.5 mm. and 0.45 mm. in diameter. In *S. Suessii* Zeill. the megaspores are 0.50-0.65 mm. in diameter and are provided with an equatorial flange like that on the spores of *Selaginella caulescens*, while the microspores have a diameter of 0.04-0.06 mm. In this French species from the Coal-measures (Stephanien) of Blanzy there are 16-24 megaspores in the megasporangia.[2] In *Selaginellites Dawsoni* the number has not been determined.

Several Cretaceous and Jurassic species of *Lycopodites* have been described from British and foreign localities, but without information as to the nature of the spores it is impossible to assign them to a definite position in the Lycopodiales.

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[1] Halle ('07), p. 9.

[2] Zeiller ('06), p. 141, Pls. xxxix-xli.

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EXPLANATION OF PLATE IV.
ILLUSTRATING PROFESSOR SEWARD'S PAPER ON "A BRITISH FOSSIL *SELAGINELLA*."

Selaginellites Dawsoni sp. nov. (The author is indebted to Mr. Hamshaw Thomas for the photograph reproduced in Fig. 7. Figs. 1-2 were drawn by Mr. Brock and Figs. 3-6 are from photographs by Mr. Tams).

Figs. 1, 1a. Sterile Shoot. Fig. 1. Nat. Size; Fig. 1a, × 3.
Figs. 2, 2a. Fertile Shoot. Fig. 2. Nat. Size; Fig. 2a, × 3.
Figs. 3, 4, 5. Microspores. Figs. 3, 4, × 300; Fig. 5, × 100.
Fig. 6. Megaspore, × 100.
Fig. 7. Megaspore and microspores, × 100.

THE EVOLUTION OF THE HIGHER UREDINEÆ.

By W. B. Grove, M.A.

[With Two Figures in The Text].

ONE of the most pregnant phenomena attending the study of the Uredineæ during the present century has been the discovery by Tranzschel of the heterœcism of *Puccinia Pruni-spinosæ*, the Plum Rust. He proved what was previously not even suspected, that it has its æcidial stage on *Anemone coronaria*. But it is not the *fact* of the discovery, but the *method* which led up to it, that is of the greatest importance. This method has already led to several important results and will undoubtedly lead to numerous discoveries in the future, but its present advantage is that it gives us a view of the evolution of the Uredineæ which is based upon certain facts, and not upon uncertain speculations.

The facts are these:—In Europe and North America *Anemone nemorosa* bears a Micropuccinia, known as *Puccinia fusca* Winter, which has teleutospores of a very uncommon character (Fig. 1, A),—they have the two cells for the most part globular (especially the upper one), divided therefore by a deep constriction, easily separating from one another, covered all over with rather large coarse warts, and attached in bunches of 10—20 by short pedicels to a common base. The teleutospores are accompanied by spermatia, but by no other spore forms. Now the teleutospores of *P. Pruni-spinosæ* (Fig. 1, B) on *Prunus* are absolutely identical with these, although they are accompanied (contrary to those of *P. fusca*) by uredospores and not by spermogones. These uredospores (Fig. 1, C) are also of a very uncommon shape; they have the cell-wall conically thickened at the apex (after the style of many teleutospores of *Uromyces* or *Puccinia*), and are provided with downward-turned spines which are larger in the lower half of the spore than towards the summit. They are in fact closely similar to *amphispores*. They are also accompanied by numerous capitate paraphyses. Furthermore, there is on *Anemone coronaria* an æcidium (*Æ. punctatum* Pers., *Æ. quadrifidum* DC.) accompanied by spermogones, which had hitherto stood isolated, not being followed by any other spore-form on the same plant. It occurred to Tranzschel, *reasoning merely from the similarity of the two teleutospores*, that this æcidium belonged to *P. Pruni-spinosæ* (24). The idea was without delay proved by experiment to be a fact, which has since been substantiated by other observers (3). Thus it is shown that *P. Pruni-spinosæ* is a heterœcious species, having its spermogones and æcidia on *Anemone* and its uredo- and teleutospores on *Prunus*.

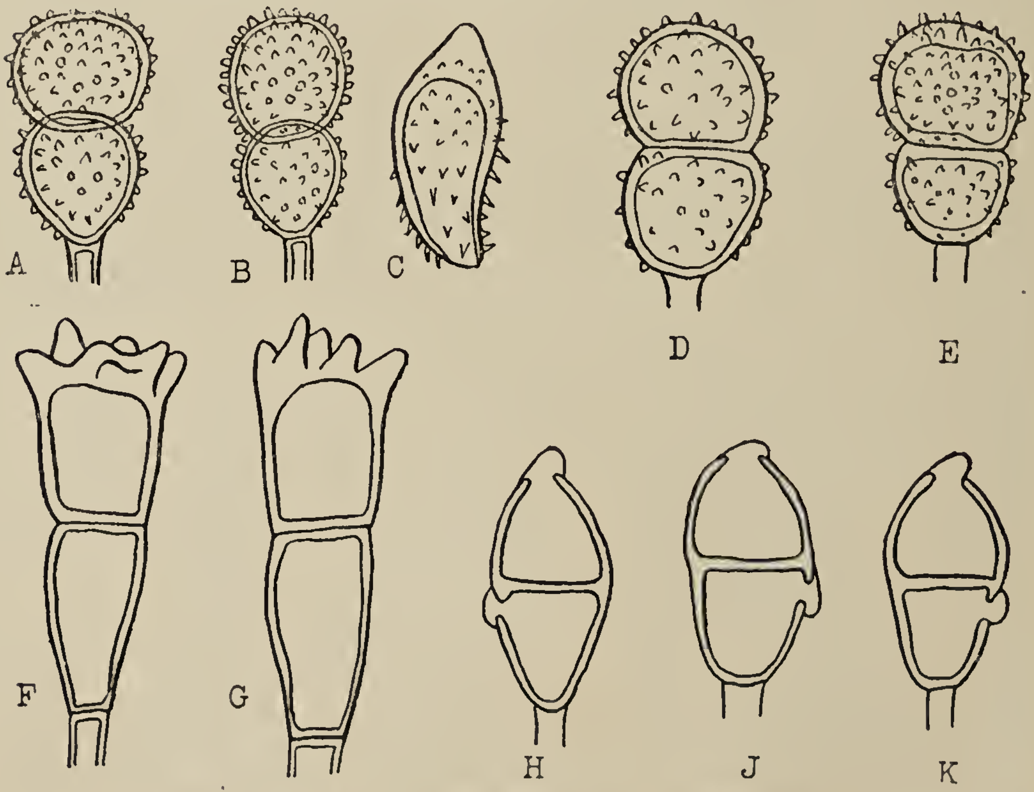

Fig. 1. Teleutospores of *Puccinia fusca* (A), *P. Pruni-spinosæ* (B), *P. cohæsa* (D), *P. Thalictri* (E), *P. coronata* (F), *P. Mesnieriana* (G), *P. albescens* (H), *P. Adoxæ* (J), and *P. argentata* (K), and Uredospore of *P. Pruni-spinosæ* (C). D is from an original specimen collected by Long. H, J, and K are selected specimens, but are fairly representative of each type. A to G, × 660; H, J, K, × 900.

To explain this state of things it was suggested that there was originally a complete autœcious species of *Puccinia* which had its spermogones, æcidiospores, uredospores and teleutospores on *Anemone*. From this, we may suppose, there could arise (1) a species of Micropuccinia on the *Anemone* with teleutospores only, the other two useful spore-forms being suppressed, but the useless[1] spermatia still lingering as a survival or legacy from the past, (2) a species which still retained its spermogones and æcidia on *Anemone* but which had transferred its uredo- and teleutospores, by a sudden mutation, to various species of *Prunus*.

Putting aside, for the moment, the consideration of the reasonableness of the suggestion, the possibility of such an evolution cannot be gainsaid. The mutation is possible, because the æcidiospores, being produced in enormous numbers at a certain period, must be spread over all the leaves of plants belonging to the same association within a certain radius; there they might germinate, the germ-tube would penetrate through a stoma if it could, and having once gained access to the stores of nutriment contained in the cells within would draw upon them for its food supply, if their mutual chemical and vital attractions and repulsions would permit it to do so. Untold millions of æcidiospores go through this experience annually, and untold millions fail; but that is no reason why, at rare intervals, when every circumstance is favourable, one of them should not succeed in establishing itself upon the new host. It is known that the æcidiospore is rejuvenated by the effect of the presence in it of two non-sister nuclei, and as Olive says (20) we should expect the heterœcism to arise, if at all, just at that point of greatest vigour. It is also known that germ-tubes can enter the stomata of plants other than their proper hosts (13): their further growth would demand a certain chemical affinity in the cell-contents of the two hosts, and probably also a slight change (mutation) in the cell-contents of the spore itself, such as we know, from Marshall Ward's experiments on *Puccinia dispersa*, to occur at intervals.

So far, however, this is mere supposition: but there is more to follow. If the imagined autœcious species on *Anemone* ever existed, it might still remain, in some corner of the world, if not in Europe. There *is* a very rare species, first described in 1902, on *Anemone decapetala* in Texas but found nowhere else, which answers to the exact requirements. This is *P. cohæsa* Long. Its spermogones and æcidia agree in every detail with those on *Anemone coronaria*, e.g., among other resemblances, in both the spermogones are similar in shape and distribution, and the margin of the æcidial cups breaks up into a few (usually four) spreading lobes—a very unusual circumstance from which *Æ. quadrifidum* derived its name. Its uredo- and teleutospores (Fig. I, D) agree equally with those on *Prunus*, the sori are the same in size and arrangement, both kinds of spores have the same unusual shape and the same surface markings, and the uredospores are accompanied by numerous capitate paraphyses. Finally, there is one particular detail of agreement which must convince the most cautious—the teleutospores of both occur in bunches of 10—20 together, all attached by short fragile pedicels to a common base. Arthur includes both species (*P. cohæsa* and *P. Pruni-spinosæ*), on this and other grounds, in his genus *Tranzschelia* (1). It is probable, though no investigation has been made, that in these cases the teleutospore-mother-cells bud off in succession from a common basal cell, as takes place in a smaller degree in *Leptinia* and *Chaconia* (15) and, as shown by Hoffmann (14), in *Endophyllum*, and by Dittschlag, in *Puccinia Falcariæ* (10).

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[1] All the numerous attempts that have been made to convey infection by means of the spermatia have uniformly failed.

Such a wonderful series of congruences suggests at once a reasonable explanation. *P. cohæsa* represents the original species. From this *P. fusca* arose by a shortening of the life-history (by dropping out some of the spore forms), a process which is now well known to indicate an adaptation to an environment in which the saving of time is of importance, as in Alpine districts or on early spring vegetation, such as in the case of *Anemone*. In Switzerland the percentage of Micropucciniæ is twice as great in the Alpine as in the lowland regions; the same is true of the flora of Sweden when compared with that of Germany (12). Secondly, *P. Pruni-spinosæ* arose by a sudden transference of the uredo- and teleutospore phases to another host, as outlined above. In this we can trace an agreement with Dietel's "Law." He arrived at the conclusion (9), by studying the sequence of the Uredineæ, that they have evolved *pari passu* with the plants upon which they are parasitic and, as a corollary, that when a mutation took place, leading to a change of host, it was almost always in the direction of selecting the new one from a group of later (or at any rate, not of earlier) evolution than the original host. In consonance with this is the fact that the Rosaceæ, to which *Prunus* belongs, are of a more specialised type than the Ranunculaceæ, to which *Anemone* belongs.

It is true that there are several apparent exceptions to the "Law," as in *Gymnosporangium*, which has its æcidial stage on Rosaceæ and its teleuto-stage on the Junipers. The "Law" is, in fact, only an empirical, but widely applicable "Rule."

Again, there are other Micropucciniæ which have teleutospores of exactly the same type as *P. fusca*, viz., *P. suffusca* Holw., on other species of *Anemone*, and *P. Thalictri* Chev. (Fig. 1, E) on species of *Thalictrum*, in Europe and North America—and on the other hand æcidia of the same type as *Æ. punctatum* and considered as equally belonging to *P. Pruni-spinosæ* have been found in North. America on *Thalictrum* and *Hepatica* (1). All these are survivals from one ancestral species which at one time ranged widely over Ranunculaceæ of the tribe Anemoneæ, and of which we can predicate that it was autœcious, had all four spore-forms, the æcidia with a broad usually four-cleft margin, the uredospores thickened at the summit and more echinulate below than above, the teleutospores of two globose cells which separated easily and were adorned with numerous prominent and coarse warts, and possibly had its teleutospore-mother-cells produced in large clusters by budding from a common base. The remarkable fact is that, apart from the species here mentioned, these spore-characters are met with in the genus *Puccinia* only very rarely, and never all associated in this same way.

P. coronata and its close ally *P. Lolii (P. coronifera)*, which are known from all parts of the world except Africa, afford another instructive, though not equally convincing, example. Here we have a species[1] having its æcidia (spermogones appear to be wanting) on *Rhamnus*, and its uredo- and teleutospores on *Holcus* and other grasses. The teleutospores (Fig. 1, F) have at their apex a number of finger-like processes which impart to them an unusual appearance; *P. coronata* var. *himalensis* Barcl. (from Simla) has its æcidia on another species of *Rhamnus* and its fingered teleutospores on another grass *(Brachypodium)*. On *Rhamnus* there are two species of *Puccinia* which have teleutospores only, *P. Mesnieriana* Thüm. (Fig. 1, G) from Portugal, Teneriffe, Syria and California, and *P. Schweinfurthii* Magn. (from Abyssinia and tropical East Africa). These are the only two known on *Rhamnus*, and *both of them have teleutospores exactly like those of P. coronata.* An autœcious species on *Rhamnus*, having both æcidiospores and teleutospores, has not yet been met with; and the curious shape of the teleutospores, though very striking, is not without parallels in other not closely connected cases, e.g., *P. Festucæ* Plowr., with its æcidia on *Lonicera*, and *P. Beckmanniæ*, as well as species of *Uromyces (coronatus, phyllodiorum*, etc.). Nevertheless, the series of forms given above on *Rhamnus* and grasses bears a close similarity to that on *Anemone* and *Prunus*. If the same explanation is to apply, one must remember that the Gramineæ (and also the Cyperaceæ) are not, as has sometimes been thought, primitive families but more recently evolved ones, being derived like the Orchidaceæ from the Liliaceous type, though by different routes.

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[1] *P. coronata* and *P. Lolii* are merely "biologic" races of one species.

We find much the same relations existing in other groups of species; not to labour this point, I will refer briefly to two alone. The well-known *P. graminis* has its æcidia and spermogones on *Berberis*, and its uredo- and teleutospores on grasses all over the world. *P. Berberidis* Mont., from Chile, has æcidiospores and teleutospores on *Berberis; P. Meyeri-Alberti* Magn. from Chile and Patagonia, also on *Berberis*, has probably teleutospores only, which differ from those of *P. Berberidis* merely in having a greater length. The æcidia of *P. Berberidis* are not unlike those of *P. graminis*, but in the former case teleutospores are produced round the æcidial cup, obviously from the same mycelium (6.) There is also *P. Arrhenatheri* Erikss. (from Europe and Western Asia) which has its spermogones and æcidia on *Berberis* and its uredo- and teleutospores on *Arrhenatherum elatius*. The teleutospores of this species are similar to those of *P. graminis*, but on *Berberis* its perennial mycelium causes witches'-brooms, while the æcidium of *P. graminis* does not. Mention must also be made of *Æcidium Maghellanicum* and *Æ. Jakobsthalii-Henrici*, both on *Berberis* and from the antarctic regions, of which *Æ. Maghellanicum* causes no witches'-brooms, but the other does; their teleutospores are unknown. All these may be descendants of one ancestral autœcious species which grew on *Berberis* and of which the uredo- and teleutospore phases migrated to the Gramineæ, again without violating Dietel's " Rule."

The second instance is that of *P. Caricis*, which has its æcidium on *Urtica* and its teleutospores on *Carex*. Here also we find a Micropuccinia on *Urtica (P. Urticae* Barcl., from Simla) which has teleutospores only, similar to those of *P. Caricis* but occurring in dense clusters on coloured spots like those made by the mycelium of the æcidium of the latter on *Urtica*, and therefore, in a manner quite unlike the teleuto-sori of *P. Caricis*. In this connection it may be as well to call attention to the fact that, in many cases, the form of the sori and the colouring of the spots on which they stand are determined by the nature of the host rather than by that of the parasite. The chief guide in classification must always be the *form* of the teleutospore. Dietel's "Rule," it will be observed, is again not broken.

PUCCINIÆ ON ADOXA.

Another case of a highly involved, but slightly different, nature must now be considered. On *Adoxa Moschatellina* in this country (a *spring* flowering plant) there is found an æcidium, accompanied by spermogones and sometimes followed on the same plant by a few scattered teleutospore-sori which contain also a small number of uredospores; this is called *P. albescens* Plowr. (Fig. 1, H), There is also found on the same host a *Puccinia* (*P. Adoxæ* Hedw. f.), which produces only teleutospores in densely crowded sori (Fig. 1, J). These two forms appear to be almost always separated: one attacking *Adoxa* in one district, and the other in another district, not only so in England, but also on the Continent. Moreover, these teleutospores of *P. Adoxæ* begin to appear abundantly in early spring (March) at the same time that the æcidia of *P. albescens* are appearing in their district, while the few teleutospore-sori of the latter do not appear till May. Thirdly, there is a *Puccinia* (*P. argentata* Wint.) which has its spermogones and æcidia on *Adoxa*, but its uredo- and teleutospores (Fig. 1, K) on *Impatiens;* these latter have been found in only one district in this country. The heterœcism in this case has been fully demonstrated by Bubák (4). The teleutospores of all three are almost exactly alike, and although an attempt has been made by Bubák to distinguish the two æcidia by the colour of the spores, the distinction is of little value, even if not, as I am inclined from my experience to think, quite untrue. Some authors unite the two former species, but this does not meet with general approval, and the most natural conclusion from the known facts is that we have here a mutating species which has not yet completely specialised itself into three forms—*P. albescens*, a complete autœcious species on *Adoxa* (Auteupuccinia); *P. argentata*, a Hetereupuccinia on *Adoxa* and *Impatiens*; and *P. Adoxæ*, a Micropucccinia on *Adoxa*.

The first of these would in that case represent the original form, from which the other two are being evolved. In North America, an æcidium on *Adoxa* is found, but the teleutospores are, at any rate, excessively rare on that plant (there seems to be only *one* record), while those on *Impatiens* are common. It appears reasonable to suggest that the fungus is becoming specialised as heterœcious in North America, where *Impatiens* is abundant, while it is continuing to be autœcious in this country, where *Impatiens* is very rare, although it is at the same time evolving here a Micropuccinia which has not yet been found in America. We have, in fact, a case parallel to that diverse evolution of the biological races of *P. graminis* which is taking place at the present time in three distinct directions in Europe, North America and Australia respectively.[1] Whether the Balsaminaceæ, to which *Impatiens* belongs, are to be considered as of a higher type than *Adoxa* is a matter about which there might be two opinions, if *Adoxa* is placed among the Caprifoliaceæ; personally I should have little hesitation in putting the Balsam, with its complicated floral and fruiting mechanism, far above the simple little Moschatel.

SUB-DIVISIONS OF PUCCINIA.

Before we conclude that the theory suggested by these examples (which might be largely increased) is fully justified, there are other aspects of the question to be considered. It is obvious that the great genus *Puccinia*, comprising now about 1,300 described species, must sooner or later be divided—whether into sections, sub-genera, or genera, matters not. Even in the 130 species of our British flora, some sub-division is necessary for the sake of clearness. Four attempts at such arrangements have been made. Schröter (22) instituted the sections Eupuccinia, Pucciniopsis, Brachypuccinia, Hemipuccinia, Micropuccinia, and Leptopuccinia, based upon the number and nature of the spore forms known. Thus, designating spermogones by O, æcidia by I, uredospores by II, and teleutospores by III, his sections may be defined (in the light of our present knowledge) as follows :—

Possessing		
O, I, II, III	Eupuccinia	Auteupuccinia, all on the same species; Hetereupuccinia, O and I on one species, II and III on another.
O, I, III	Pucciniopsis.	
O, II, III	Brachypuccinia.	
II, III	Hemipuccinia	Possibly most (though not all) of these will be found in the future to be heterœcious.[2]
[O] III	Micropuccinia	Spermogones not always occurring.

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[1] In Australia, according to McAlpine (17), *P. graminis* has completely lost the power of infecting the Barberry, which is not a native of that country.

[2] It would seem possible to determine whether a supposed Hemipuccinia belongs to a heterœcious species or not, by cytological investigation. If the first-formed mycelium of the uredo-stage is binucleate, the fungus in question must be a stage of a heterœcious species: if not, if the binucleate condition arises in the course of development of the uredo, then it is a true Hemipuccinia. Of the fourteen species included under this head in Plowright's Uredineæ (21), five have been already proved to be heterœcious, and three others are strongly suspected to be so.

The Leptopucciniæ are omitted: there is not a special group of that kind. Schröter defined it as the group in which there are teleutospores only which germinate as soon as mature. But this is not absolutely true; most, if not all, the Leptopucciniæ possess spores of both kinds, some which germinate at once, and others which do so only after the winter's rest, e.g., *P. Veronicarum.* We should speak of lepto-forms of the groups: e.g., *Endophyllum Sempervivi* is a lepto-form.

Since this classification depends upon the number of known spore-forms, it is evident that a species must be changed from one section to another as our knowledge of it increases, e.g., *P. Pruni-spinosæ* was to Schröter a Hemipuccinia, now it belongs to the Hetereupucciniæ, while *P. cohaesa* belongs to the Auteupucciniæ and *P. fusca* to the Micropucciniæ. Schröter's classification does not indicate affinity in any degree; its sections cannot have the force of sub-genera.

Another more recent attempt at classification is that of the brothers Sydow (23). They arrange the species according to their hosts, beginning with those on the Compositæ and ending with those on the Gramineæ. In passing, there should be noted the false implication that the Compositæ are the most highly evolved order and the Gramineæ the least so. Here also allied species are occasionally widely separated, e.g., *P. fusca* and *P. Pruni-spinosæ*, though *P. fusca* and *P. cohæsa* are brought close together. Their method is excellent as an index, and is, indeed, employed by them on that ground; but it cannot be used in any other way, although it does in a large number of cases bring allied species together, simply because many of those parasitic upon allied genera or species have been evolved *pari passu* with the latter from a common ancestor respectively.

A third attempt is that of Fischer (12), who takes the form and markings of the teleutospore as his basis, but combines it with the grouping of the parasites according to their teleutospore hosts, or with the biological distinctions of Schröter. This is a great advance, because it brings together allied species, not only in the case of *P. fusca*, *P. suffusca*, *P. Thalictri*, but in many others; even if the heterœcism of *P. Pruni-spinosæ* had been known in time, however, it might still have been separated from its allies.

A fourth attempt is that of Arthur (1), who bases his genera, e.g., *Tranzschelia*, upon the number of spore-forms known combined with other morphological characters. This is also an approach to the ideal classification, but it is subject to the same fatal objection as Schröter's. Arthur, for instance, separates *P. fusca* from *P. Pruni-spinosæ*, placing it in his genus *Polythelis*, though he brings *P. cohæsa* and *P. Pruni-spinosæ* together. If a method of classification is only correct in so far as it coincides with the groupings that have originated in a line of descent, then no such method can be satisfactory that does not place these three species in a common genus.

DIETEL'S RULE.

To illustrate Dietel's " Rule," we may consider the numerical relations of the species of *Puccinia* and *Uromyces* (the two highest evolved genera of the Uredineæ) to their hosts. The number of Dicotyledons in the world is to the number of Monocotyledons about as 5 : 1; the number of Pucciniæ parasitic on Dicotyledons is to the number on Monocotyledons about as 2 : 1; in the genus *Uromyces* the proportion is about the same (23). In other words, the distribution of the parasites has not yet attained so great an extension on the higher class as on the lower. The evolution of the parasites naturally lags behind that of the hosts.

The species of Pucciniæ on the Compositæ number over 300, *i.e.* nearly one-quarter of the known total. In Britain the number on Compositæ is also about one-quarter of the British Pucciniæ. The species of *Uromyces* on Leguminosæ number about 120 out of over 500 in the world; *i.e.*, again about one-quarter: the proportion in Britain is much the same. If the species of *Uromycladium*, all on *Acacia*, are included (and this genus differs from *Uromyces* mainly in bearing its teleutospores not singly, but in clusters upon a common stalk) then the world-proportion would be over one-quarter. The striking point is that the greatest number of each genus lives on orders belonging to the largest and most highly evolved sections of the gamopetalous and polypetalous groups respectively. *Puccinia* seems to have specialised upon the Compositæ in colder lands, and *Uromyces* upon the Leguminosæ in warmer lands, for the species of *Puccinia* on the latter are hardly more than 1%, and of *Uromyces* on the former about 6%, of the totals.

The number of *Pucciniæ* on the Grasses is about 150, and of *Uromyces* about 50; *i.e.*, in each case in the neighbourhood of 10%. The relations of the numbers of these genera to other families are equally interesting, but would take too long to unravel here. It is worthy of mention, however, that there are few on the Rosaceæ, and none at all on the Salicaceæ or the Coniferæ, though Uredineæ of lower type are frequent on those Orders. This shows that, as the more specialised orders of angiosperms arose in the course of evolution, fresh parasites of a higher type were evolved to suit them.

SPORE-FORMS AND THEIR RELATIONS.

In speaking of the Micropucciniæ so far, it has been assumed that the existence of species with *one* spore-form arose by suppression of the others. But reduction alone is never capable of providing a full explanation of the evolutionary process; there must always have been an advance in complexity first. If we consider Schröter's classification we see that the one spore-form which runs through the whole series is the teleutospore (including, of course, the basidiospore which is its invariable product); this is present in every case, whatever else may be absent.[1] It is natural to conclude that this is the essential and ancestral type of spore.

But if the theory of Blackman and others that the æcidium represents a remnant of a formerly existing sexual process is accepted, as it must be, then a spore produced like the æcidiospore must also be one of the ancestral types.

Again, there are many grounds for assuming that the æcidiospores, uredospores, and teleutospores (and even the spermatia as well) are all modifications of one common spore-form. The formation of spermatia in the spermogone takes place much in the same way as that of æcidiospores in the æcidium, except that there are no intercalary cells. In certain cases *primary* uredospores take the place of æcidiospores, being followed by *secondary* uredospores, alike in form but differing in the character of the sorus, and probably in all such cases the primary uredospores alone are accompanied or preceded by spermogones, as in *P. obtegens.* Another species, *P. Podophylli*, has primary and secondary æcidiospores, the latter taking the place and function of uredospores. In *Uromyces Veratri* similar spores, if sown upon young leaves produced only uredospores; if on old or sickly leaves produced more teleutospores (18). It is well-known that teleutospores are commonly borne upon the same mycelium as uredospores; but also æcidiospores can be followed by teleutospores upon the same mycelium, even within the æcidial cup, as in *U. Cunninghamianus* (2), or close to its margin, as in *Puccinia Berberidis* (6), or in a circle round it, as in *Uromyces Betenis*. The pedicel of the uredo- and teleutospore is the homologue of the intercalary cells of the æcidiospore-chain. In the sori of the primary uredospores of *Phragmidium Potentillæ-canadensis* (= *Ph. Tormentillæ* Fckl.) the basal cells act as in the formation of æcidiospores, but the lower sterile half of the spore-mother-cell, instead of disintegrating, elongates to form the pedicel of the uredospore. Large basal cells, similar to those occurring in the æcidium, are frequently found in the sori of uredo- and teleutospores. In many of the lower Uredineæ those two kinds are produced in chains. In *Chrysomyxa*, æcidio-, uredo-, and teleutospores are all concatenate. We have thus various requirements to be satisfied by any explanation of the origin of these spores: is it possible to reconcile them all?

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[1] Isolated "species" of Uredo and Æcidium are ignored, because there is reason to believe that all, or nearly all, of these will be assigned to other species as our knowledge of them increases. Of the 38 "imperfect species" recorded in Plowright's Uredineæ, only four are now still unassigned.

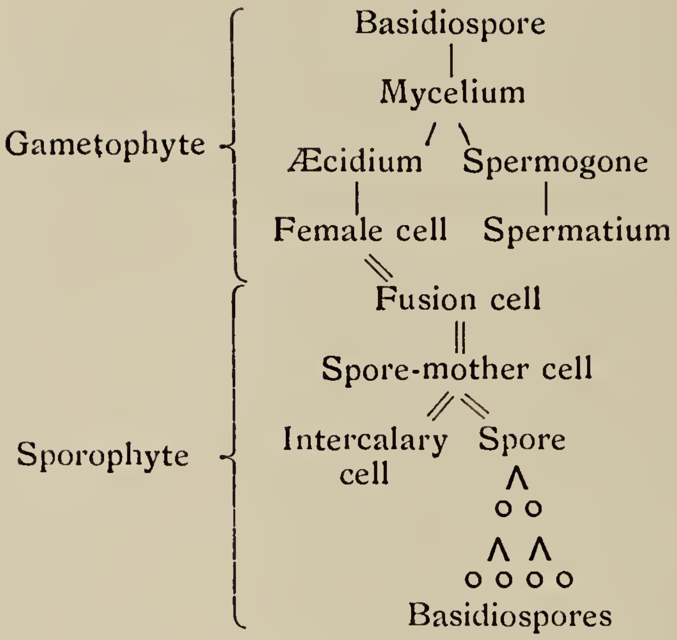
ENDOPHYLLUM.

The genus *Endophyllum* comes to the rescue, especially since the recent investigations of Hoffman (14). He shows that *Endophyllum Sempervivi* has only one kind of spore in addition to the spermatia and basidiospores. This is produced in a cup exactly like an æcidium, in chains with intercalary cells, from a basal fertile cell with two nuclei, which arises as in *Phragmidium*, etc., by the fusing of two of the cells of the fusion-tissue after the manner described by Christman (5); the two which fuse are adjoining cells of the same mycelium (not situated in any definite plane), but presumably never of the same hypha. The pair of nuclei then divide in the well-known conjugate way, the æcidiospores thus all containing at first two non-sister nuclei which afterwards fuse as the spore approaches maturity. This fusion has been denied by Sapin-Trouffy and Maire, but evidently as the result of mal-observation: their mistake has led to several unfounded conjectures about *Endophyllum*. The æcidiospore germinates as soon as mature with a basidium and basidiospores, like an ordinary teleutospore of *Puccinia*, the fusion-nucleus having sooner or later divided twice, the first being the reduction-divivision. The spores of *Endophyllum Euphorbiæ* do the same.

Obviously these spores are at once æcidiospores by the mode of their formation, and teleutospores by the mode of their germination. Here, then, is one at least of the ancestral types of spore among the higher Uredineæ; the lower group, the Melampsoraceæ, which demands a separate treatment, is excluded from present consideration. It should be noted that, even before its nuclear history was properly investigated, *Endophyllum* was rightly considered to be one of the highest forms of the lower group or of the lowest forms of the higher group, if with Dietel we suppose the Uredineæ to consist of two groups, the Pucciniaceæ and the Melampsoraceæ, or, as I have named them, the Pedicellatæ and the Impedicellatæ. Moreover, Hoffmann shows that the basidium of *E. Sempervivi*, sometimes bears more than one basidiospore from each of the four cells. He observed as many as eight from one basidium. We may conclude that this is the primitive mode of basidiospore-formation, resembling in that respect that of the Ustilagineæ, from the ancestors of which it is generally agreed the Uredineæ are descended. I have not been able to meet with this mode in *E. Euphorbiæ*; in that species, so far as I have seen, there is always one basidiospore on each of the four cells. Müller's experience seems to be the same (19).

We may now take it as established that *Endophyllum* approaches the form of the primitive Pucciniacea, though undoubtedly it has a more highly developed peridium. The latter, therefore, had on the same mycelium spermogones producing male spermatia, and female cells arranged in a more or less cup-shaped chamber. At some time or other, either before or after this, fertilisation by the spermatia was lost, and the conjugation of two equal female gametes took its place. The resulting spores were produced in chains, with intercalary cells to facilitate dispersal—these on germination produced a basidium and basidiospores, each of which could infect the host again, and produce a mycelium which again bore spermogones and æcidia. Hoffmann proved that this is so in the case of *Endophyllum Sempervivi*. It may be noted that in the Ustilagineæ there is, in addition to the conidia, only one kind of spore which acts like the teleutospores of the Uredineæ.

The sterigmata of *Endophyllum* are variable in size and indefinite in shape. This is itself a sign of a lower stage of evolution; in the higher types of the Uredineæ the basidium was modified so as to produce only one basidiospore from each cell of the basidium and on a well-defined sterigma. The life-cycle of *Endophyllum* may be represented diagrammatically, much as is done by Hoffmann, in the following scheme:—



This hypothesis of the primitiveness of an *Endophyllum*-like Uredine was propounded by Barclay (2) but, since in his day the nuclear history of the Uredineæ had not been at all investigated, it was devoid of that strong confirmation which the researches of Hoffmann have now afforded it. Barclay shows how, in *Uromyces Cunninghamianus*, only the primary æcidiospores are accompanied by spermogones; these æcidiospores, when mature, germinated sometimes by a kind of abortive basidium which became uni-septate, but instead of producing basidiospores each cell gave rise to a germ-tube[1], which would enter the host (presumably through a stoma) and there produce a mycelium which would give rise to the secondary æcidiospores; these might then repeat the process or *be followed within the same cup* by teleutospores.

This enables us to picture exactly how the first step of the separation of teleuto- from æcidiospores could originate; the transformation of these secondary æcidiospores into uredospores would then be a simple change. It must be remembered that the spores of *Endophyllum* germinate at once; on that account the fungus hibernates by its mycelium in the growing points of the host, a comparatively inefficient method. The separation of æcidio- from teleutospores, and the consequent intercalation of spores devoted entirely to the spreading of the parasite, would enable the teleutospore more easily to become a resting spore, and thus increase the ability of the fungus to adapt itself to fresh conditions. The intercalation is, as was to be expected, a lengthening of the sporophytic generation.

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[1] When teleutospores germinate in water, deprived of air, they generally produce long tubes, and not infrequently no basidiospores.

When the sporophytic generation was still further lengthened, by the introduction of uredospores, it is certain that, of those which had all the three spore-forms, the autœcious species would be first evolved. There are then three possible hypotheses by which the origin of heterœcism could be explained. The *first* is due to Dietel, (7) and agrees with the one suggested at the beginning of this article. It is approved by Klebahn (16). The *second* is Dietel's later alteration of his hypothesis (8) : he supposes that the primitive form of any group of species possessed only teleutospores, and was confined to one host: the present state of things arose (1) by intercalation, (2) by an accompanying mutation signified by the migrating of the æcidiospores on germination to a new host. This is also incorporated in the hypothesis here advocated, although in a sense not conceived by Dietel. The *third* is due to Fischer; (11) he supposes that the primitive form was plurivorous and possessed all spore-forms: then a further development took place by which some of the evolved species restricted certain of their spore-forms to hosts of particular families and the others to hosts of other families (*i.e.*, became heterœcious), while at the same time by suppression of some of the spore-forms Micropucciniæ and Brachypucciniæ arose. Thus, to return to the case of *Puccinia fusca* and its allies, the primitive form would be supposed to possess all spore-forms and to occur with all of them indiscriminately on Anemoneæ and Pruneæ. While certain abnormal cases might, perhaps, be more easily explained on this hypothesis, it labours under several difficulties. In the first place, it affords no explanation of Dietel's "Rule," and in the second there does not seem to exist a species of Uredineæ which is plurivorous in the required sense, *i.e.*, has all its spore-forms equally and indiscriminately on hosts belonging to diverse families. While the other hypotheses do not explain all the known cases, *e.g.*, that of *Puccinia Isiacæ*[1] or *Uromyces Scirpi*, they can, at any rate, as shown above, present actual instances of existing species which satisfy the theoretical requirements.

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[1] *Puccinia Isiacæ* has its teleutospores, so far as is known, on *Phragmites* alone, but its æcidia have been produced by Tranzschel on twenty-one plants belonging to nine widely different families, ranging from Cruciferæ to Scrophulariaceæ. Manufactured instances, however, are not much to the point.

The views here put forward concerning the evolution of the Uredineæ are expressed diagrammatically in the accompanying figure (Fig. 2).

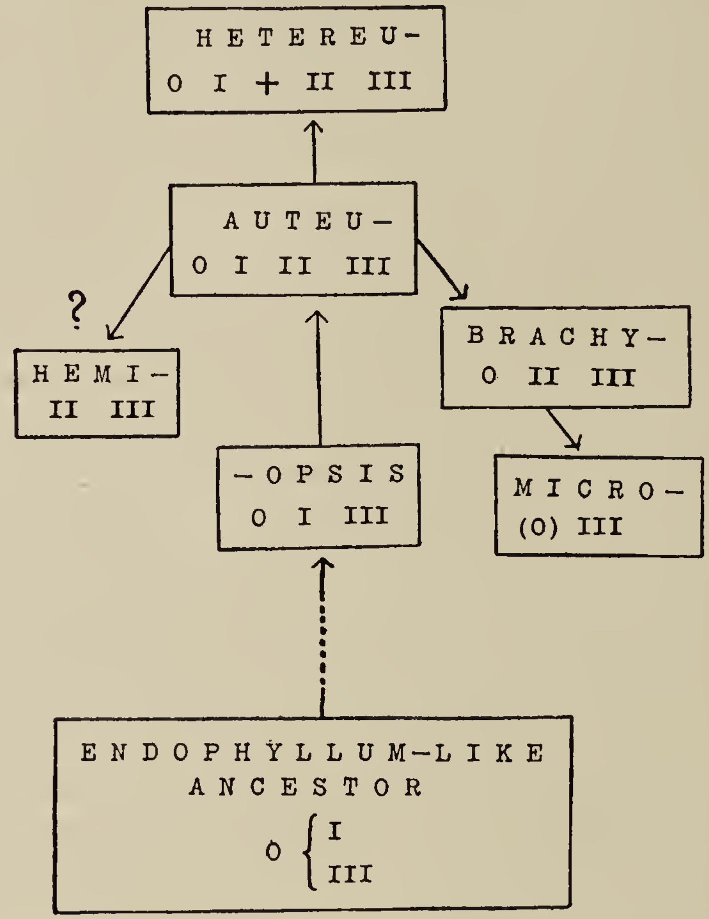

Fig. 2. Diagram representing the Evolution of the higher Uredineæ.

EXPLANATION. The prefixes and suffix can be applied to any genus. Taking *Puccinia* as an example: Pucciniopsis represents the stage when the primitive æcidio-teleutospore is divided into two spore-forms, an æcidiospore germinating conidially and a teleutospore germinating basidially; Auteupuccinia is an improvement upon this, because the intercalation of numerous generations of uredospores improves the facilities for dispersal; Hetereupuccinia is again an improvement, since in this case the fungus can form its spores upon hosts that completely disappear during the unfavourable period, if the alternate host survives; Brachypuccinia and Micropuccinia show adaptations in another way by shortening the development and quickening the formation of teleutospores, thus enabling the species to exist in subarctic or alpine regions—many Micropucciniæ still retain the spermogones, others have completely lost them; Hemipucciniæ are a mixed group, as explained in the text.

SUMMARY.

The conclusion at which I wish to arrive is this:—The primitive ancestors of the Pucciniaceæ possessed only one spore-form (æcidio-teleutospore) and were restricted to one host or to a series of closely allied hosts. From these arose cases like those of *P. Tragopogi* and *Uromyces Cunninghamianus*, where the æcidiospore germinated conidially and produced on its mycelium a teleutospore which germinated basidially. Barclay's account shows how this may well have arisen. Such a change would tend to an increased spread of the parasite, for the basidiospores are the most delicate possible of spore-forms and the mortality among them must be enormous. In some experiments which I have recently carried out in the open with *Puccinia Caricis* (see Journ. Bot., 1913, p. 42), it is quite within the mark to say that scarcely more, than one or two in a billion basidiospores achieved their end in infecting the Nettle. A spore which germinates like an æcidiospore has *many more chances* of establishing itself upon its victim than one which produces basidiospores.

From this to the intercalation of uredospores is but a small step. In some species æcidiospores and uredospores are almost exactly alike in size and form. We know of cases where uredospores are few and rare; the steps to those instances where uredospores are numerous and form the chief means of fresh infection are many and abundantly represented. Such cases, which include many of the *Pucciniæ* on the Grasses, often belong to widely distributed species. One can even conceive of a state of things (largely perhaps dependent upon climate) where the fungus relies entirely upon uredospores for its existence, and loses altogether the other spore-forms, at first functionally and at last morphologically. The Black Rust of Wheat (*P. graminis*) in Australia and *Uromyces Fabæ* in Ecuador seem to be approaching such a condition.

So far the fungus is considered to be autœcious. The formation of the heterœcious habit demands, on this hypothesis, a sudden, but not inconceivable mutation, of which evidence will yet be found From the complete autœcious species, on the other hand, Brachy- and Micro-forms might easily arise by the dropping out of some of the spore-forms as occasion demanded.

The reverse process of forming autœcious species with all spore-forms from those having only teleutospores of the type of *P. Ægopodii* (which has no spermogones), as imagined by Dietel in his second hypothesis, would imply the introduction of functionless gametes separately on each such occasion. The very persistence of the occurrence of the useless spermatia in so many species is a proof of their deep underlying primitiveness, and no hypothesis of the evolution of the higher Uredineæ is tenable which does not start with the existence of them and of the correlative female cells.

THE BOTANICAL LABORATORY,
UNIVERSITY OF BIRMINGHAM.

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RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

(Continued from p. 83),

OF the unicellular Chlamydomonadaceæ, *Chlorogonium* (Fig. 4, F, G, H) is probably on the whole the most primitive. In its elongated spindle-like form, this genus differs from the majority of the Volvocales, but an approach to the same shape is seen in *Carteria obtusa*, and the zoogametes of *Stephanosphæra* are spindle-shaped. In *Chlorogonium* the cell divides transversely to form a row of four daughter-cells, but these at once become elongated and slide past each other, acquiring the spindle form. Transverse division occurs in some species of *Chlamydomonas* (Fig. 4, B), though here, as in *Sphærella*, division is originally longitudinal and there is rotation of the dividing protoplast. In *Chlorogonium* the chloroplast is ill-defined and spongy and varies considerably in form, being in some cases ring-like or even spiral, hence symmetrical halving can be attained without the longitudinal division which is apparently essential in forms with a basin-shaped chloroplast; there are numerous (up to sixty) pyrenoids and about a dozen contractile vacuoles (Jacobsen, 61). *Cercidium* resembles *Chlorogonium*, but has only two pyrenoids and two vacuoles. Other simple forms are *Chlamydomonas* (Fig 4, A to D) and *Chloromonas*, the former with pyrenoids (typically one, but sometimes more) and the latter with none. Pascher's new genus *Agloë* (Fig. 4, E) is allied to these forms, but its chloroplast is peculiar in structure, resembling two conical flasks placed base to base and being H-shaped in optical section, with a pyrenoid in the middle of the transverse plate-like portion, and there are numerous contractile vacuoles. *Glœomonas* is an imperfectly known genus, probably allied to *Chloromonas* but with several chloroplasts. Various other genera have been described which probably represent offshoots from the *Chlamydomonas* type, though some of them are imperfectly known. Thus, *Coccomonas* (Fig. 4, J, K) appears to differ from *Chlamydomonas* chiefly in having a greatly thickened wall, often four-angled; *Pteromonas* (Fig. 4, L, M) is also thick-walled, the wall projecting as two lateral wings, as in the Carteriaceous genus *Scherffelia*; while *Phacotus* has a sculptured wall consisting of two loosely connected valves which separate to let the daughter-cells escape. Another elaboration is seen in *Brachiomonas* (Fig. 4, P, Q) and *Lobomonas* (Fig. 4, M, N); in the former the cell has a pointed posterior process and from its rounded anterior end there spring four recurved processes, in the latter the ovoid cell is produced into several rounded wart-like out-growths. In *Brachiomonas* (Fig. 4, R, S) the daughter-cells acquire the form of the parent before escaping (Teodoresco, 140; West, 147); as pointed out by

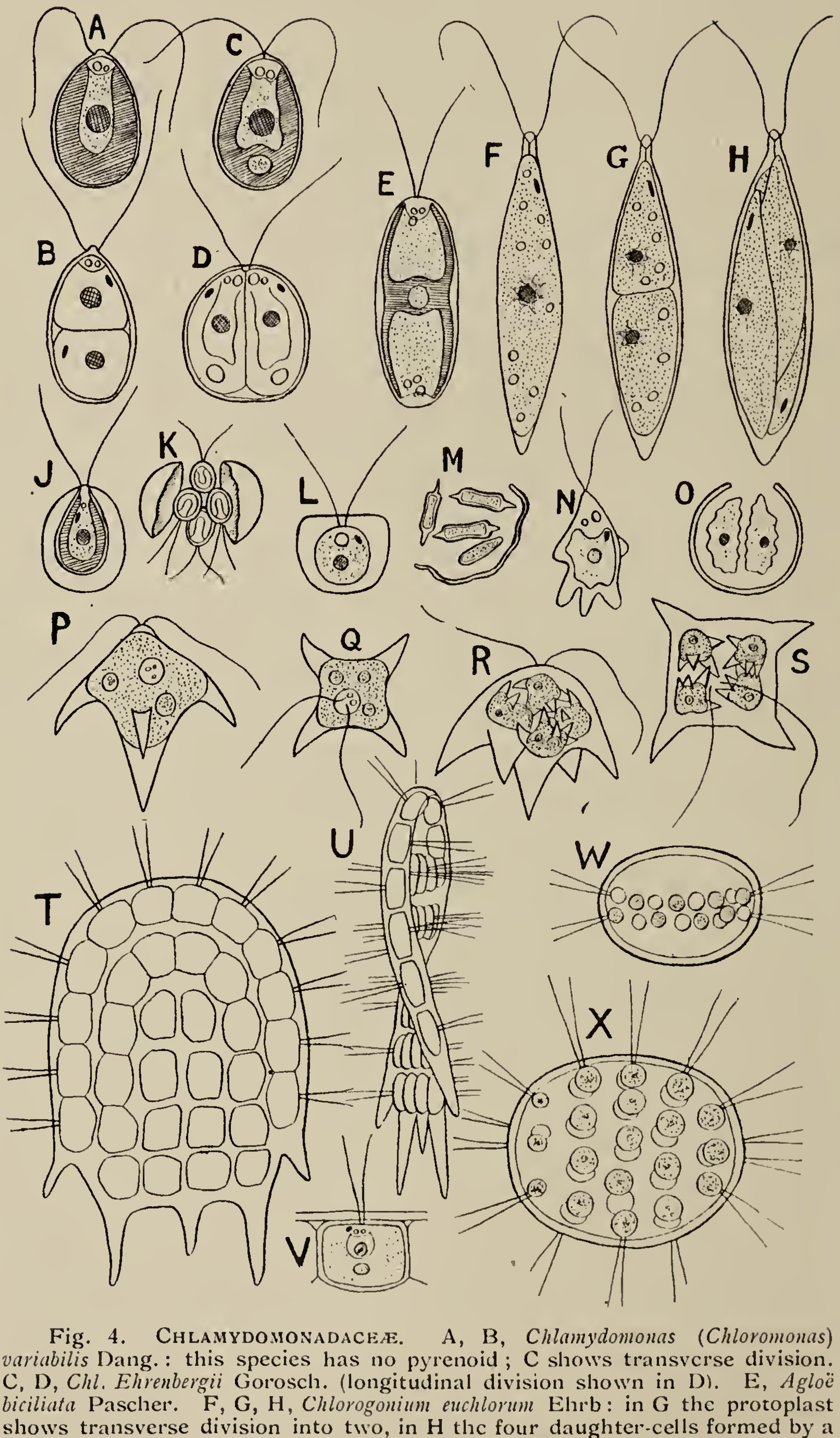

Fig. 4. CHLAMYDOMONADACEÆ. A, B, *Chlamydomonas* (*Chloromonas*) *variabilis* Dang.: this species has no pyrenoid; C shows transverse division. C, D, *Chl. Ehrenbergii* Gorosch. (longitudinal division shown in D). E, *Agloë biciliata* Pascher. F, G, H, *Chlorogonium euchlorum* Ehrb: in G the protoplast shows transverse division into two, in H the four daughter-cells formed by a further division have become arranged longitudinally within the mother-cell. J, K, *Coccomonas orbicularis* Stein: in K the wall of the resting cell has ruptured to set free the four daughter-cells. L, M, *Pteromonas alata* (Cohn) Seligo:

in M the liberation of the four daughter-cells. N, O, *Lobomonas Francei* Dang. P to S. *Brachiomonas submarina* Bohlin: P and R in side view, Q and S in anterior view; in R and S the formation of daughter cells. T to V, *Platydorina caudata* Kofoid: T, surface view; U, side view, showing the slight spiral twisting of the plate-like cœnobium; V, a single cell. W, *Stephanoon Askenasii* Schewk. X, *Pleodorina illinoisensis* Kofoid (the four small vegetative cells are shown at the left).

A to D, F to H, from Jacobsen; E, from Pascher; J, K, from Stein; L, M, from Wille; N, O. from Dangeard: P, Q, R, S, from West; T, U, V, X, from Kofoid; W, from Schewiakoff.

Fritsch (46) this recalls the autospore formation characteristic of the Scenedesmaceæ and Phytheliaceæ among the Protococcales. Included in the unicellular Chlamydomonadaceæ are two colourless saprophytic forms—*Polytoma* (Francé, 43; Prowazek, 117) which is probably derived from *Chlamydomonas*, and *Chlamydoblepharis* which resembles *Coccomonas*. In his recent classification of the Volvocales, Wille (150) includes in the Chlamydomonadaceæ the genera *Nephroselmis* and *Glœococcus*, but the former is better placed among the Cryptomonads, while the latter belongs to Tetrasporaceæ. Of the six genera appended by Wille to the Volvocales as doubtful forms, *Glœomonas* may be placed near *Chloromonas*, despite its possession of numerous chloroplasts; *Cylindromonas* and *Mesostigma* probably belong to Eugleninex, and *Tetratoma* to Carteriaceæ; *Xanthodiscus* and *Kleiniella* are still imperfectly known, though Lemmermann (85) places the former in the Cryptomonadineæ, while Francé (43) regards *Kleiniella* as allied to *Coccomonas* and *Chlamydoblepharis*.

As pointed out by Fritsch (46), of the three attempts at cœnobium formation seen in the Volvocales, that represented by *Gonium* has alone proved successful and has given rise to the remarkably complete ascending series which culminates in *Volvox*. Schussnig (133) has recently described in detail the life history of *Gonium pectorale*, and has shown that in addition to the formation of daughter colonies and zoogonidia, reproduction occurs by means of aplanospores and by the conjugation of isogamous zoogametes; while Harper (54) has carefully studied the structure and division of the *Gonium* colony. Pringsheim's observation that *Pandorina* shows heterogamy does not appear to have been repeated by recent writers on the life history of this genus; while no further observations on the peculiar genus *Platydorina* (Fig. 4, T to V) have apparently been made since its discovery by Kofoid (70) and its life history is still unknown. Schewiakoff's genera *Mastigosphæra* and *Stephanoon* (126) appear to bridge the gap between *Pandorina* and *Eudorina*, though their life history is unknown. In *Mastigosphæra*, the cells, which have but one flagellum, are less closely packed in the spherical cœnobium than is the case in *Pandorina;* while in *Stephanoon* (Fig. 4, W) the cells are arranged on the equator of the cœnobium, as in *Stephanosphæra*, but in two alternating rows. In *Eudorina* the cells are spaced out at the periphery of the spherical cœnobium, though showing a tendency to be arranged in circles, but all the cells are alike capable of reproduction, whereas in *Pleodorina* and *Volvox* there is differentiation into vegetative and reproductive cells. Until recently, *Pleodorina* with two species—*P. californica* Shaw (138), *P. illinoisensis* Kofoid (69)—was known only from the United

States, but *P. californica* has since been discovered in Ceylon (Fritsch, 46), in France (Chatton, 27), and in Java (Woloszynska, 145), while *P. illinoisensis* has been found near Heidelberg (Merton, 92), and the life history of this genus has been worked out in detail by Chatton and by Merton. In *P. illinoisensis* (Fig. 4, X) the cœnobium consists of 32 (more rarely 16 or 64) cells, arranged in five circles, the two polar circles having four cells each and the other three circles eight cells each; the cells of the anterior polar quartette are vegetative only, never dividing to form new cœnobia and are smaller than the remaining cells. This species thus forms a transition from *Eudorina* to *Pleodorina californica*, in which the cœnobium consists of 64 or 128 cells and is sharply divided into an anterior hemisphere in which the cells are purely vegetative and only one-third to one-half as large as the reproductive cells of the posterior hemisphere. In *Pleodorina* the cells have two contractile vacuoles and numerous pyrenoids, and the chloroplast is reticulate; in both species, oogamous sexual reproduction occurs as in *Eudorina*, any of the potentially reproductive cells producing either a mass of antherozoids, an oosphere, or a daughter-cœnobium. The two species of *Pleodorina* form perfect connecting links between *Eudorina* and *Volvox*, in which last genus the vast majority of the cells in the large cœnobium are vegetative and there is still more pronounced differentiation between

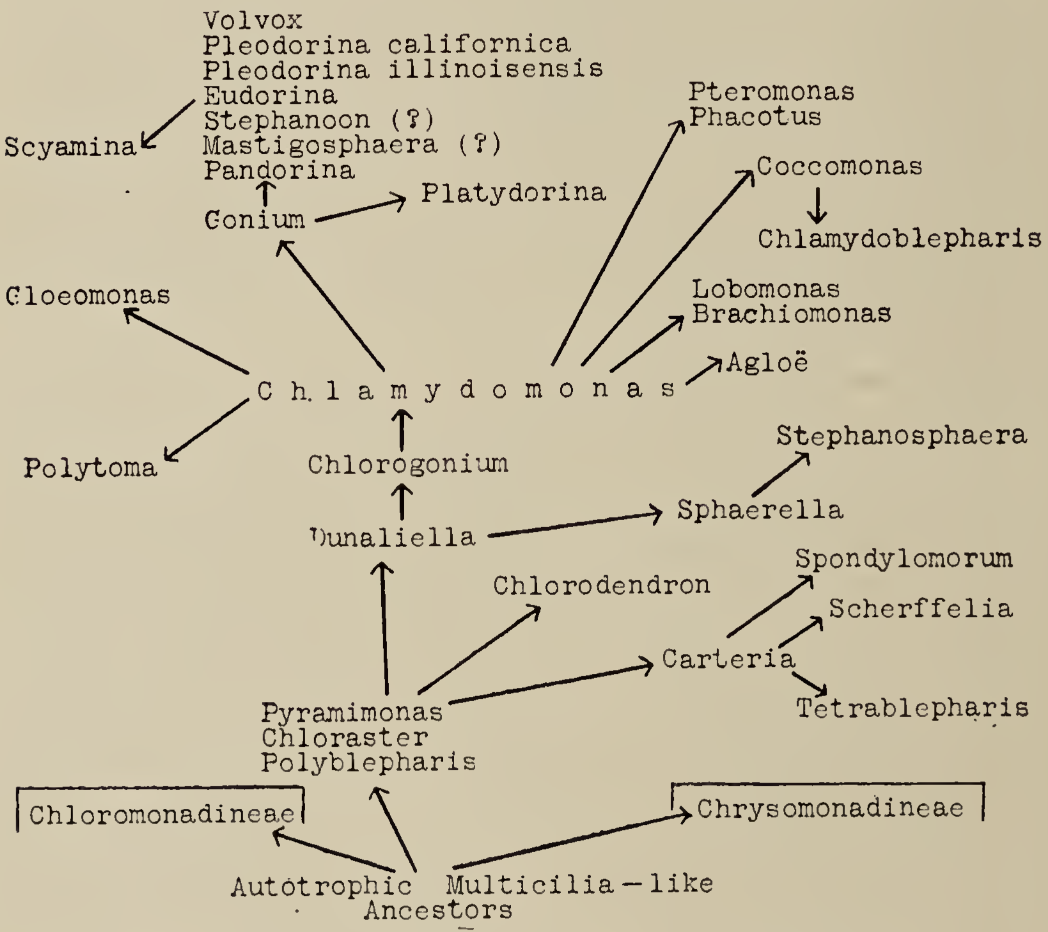

Table B.—Suggested Phylogeny of the Volvocales. For details, see Text.

the vegetative and the reproductive cells and more marked oogamy, the oogonial cells being differentiated at an early stage in the formation of the cœnobium and having no flagella. Van Tieghen's genus *Scyamina* is an imperfectly known colourless form, in which the numerous cells are placed at different depths in the spherical cœnobium, instead of being confined to the periphery as in *Eudorina;* it is quite uncertain whether it represents a saprophytic offshoot from a *Eudorina*-like type, or a form derived from *Polytoma* by cœnobial development, or indeed whether it is rightly placed in the Volvocales at all.

The inter-relationships of the Volvocales, as here suggested, are indicated on the accompanying Table B.

VI.—The Chrysomonads.

Since the publication of Senn's compilation in 1900, much work has been done on the Flagellate forms included by him in the Chrysomonadineæ and Cryptomonadineæ. From the extensive recent literature of these forms, to which Pascher has been the largest contributor, it will suffice to select for mention certain results which are of special interest in connexion with the phylogeny of the Algæ. Various new genera have been added to those enumerated by Senn, and some modifications of the earlier classification have been suggested. Senn divides the Chrysomonadineæ into three families characterised respectively by the possession of a single flagellum (Chromulinaceæ), two equal flagella (Hymenomondaceæ), and two unequal flagella (Ochromonadaceæ). Scherffel (125) has shown that *Monas, Oikomonas,* and various other genera placed by Senn in the Protomastigineæ are better regarded as colourless forms derived Chrysomonads; for instance, they show precise agreement with normal coloured Chrysomonads in producing leucosin, in the mode of encystment, and in various cytological details. In describing a new species of *Gymnodinium,* a genus belonging to the simpler Peridiniales which have been regarded as derived from the Chrysomonadineæ (see below), Ohno (94) criticises the systematic value of the flagellum number in the classification of the Flagellata. This new species differs from all other Peridiniales in having two longitudinal flagella instead of one, in addition to the usual transverse flagellum, but otherwise must be placed in the genus *Gymnodinium.* The same objection has been raised with regard to the lower Green Algæ,[1] but Senn's classification is accepted by Pascher and other recent writers on the Chrysomonads, since (as in the case of the Green Algæ) the groups are distinguished by characters other than the number of flagella. In Pascher's suggested classification (99), the Cryptomonads are merged in the Chrysomonadineæ, which are divided into four orders. The first three of these (Chromulinales, Isochrysidales, Ochromonadales) coincide with Senn's three families of Chrysomonadineæ, while the fourth (Phæochrysidales) is characterised by the possession of laterally inserted flagella—in the other three orders the flagella are terminal—and includes the Cryptomonadineæ of Senn.

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[1] See Review of Wille's classification of Green Algæ, by R.P.G., New Phytologist, vol. IX., 1910, p. 78.

The Chrysomonads are characterised by a peculiar endogenous method of cyst formation. Before a definite cyst appears, there is visible within the protoplast a membrane covered by an amœboid protoplasmic layer (Fig. 5, *11-14*), which produces sculpturing on the outer surface of the cyst membrane, but later this protoplasm retreats within the membrane through a pore which has been left, this pore being afterwards closed by a plug which in some cases consists of cellulose; the membrane usually contains silica. A similar method of cyst formation occurs in certain colourless heterotrophic genera which have hitherto been placed in the Protomastigineæ, and on this ground, as well as on account of other cytological resemblances, it is suggested that these forms should be transferred to the Chrysomonads. These forms, which may be regarded as colourless derivatives from normal autotrophic Chrysomonads—corresponding with the colourless forms (*Polytoma*, etc.) included in the Volvocales—belong to the genera *Monas*, *Oikomonas*, *Dendromonas*, *Antophysa*, *Cephalothamnion*, etc. It would appear that further investigations will lead to a considerable number of genera being transferred from the Protomastigineæ to the Chrysomonads, and doubtless to other groups of pigmented Flagellata, if we accept the view that where colourless and coloured Flagellates show close agreement in every character save the presence or absence of assimilatory pigments, the colourless forms are to be regarded as having arisen from the coloured as an adaptation to a heterotrophic mode of nutrition.

The recent work of Pascher, Scherffel, Senn, and others has shown that the Chrysomonadineæ (in the wider sense, as defined by Pascher) form a remarkably diversified group, in each order of which various parallel developments may be traced, starting from relatively simple free-living and usually small forms. The chief of these parallel developments are the formation of motile colonies analogous with those of the higher Volvocales, and of variously constructed non-motile colonies corresponding with those of the Tetrasporaceæ and other families of Protococcales characterised by aggregation of the cells into mucilaginous masses; the occurrence of amœboid forms and of amœboid phases, the latter perhaps to be regarded as reversions to an ancestral condition; the lobing, division and further elaboration of the primitively indefinite and reticulate or basin-shaped chromatophore; the coördination of the contractile vacuoles to form a pulsating vacuole system similar to that seen in the Chloromonadineæ and Euglenineæ; the substitution of solid carbohydrate assimilates (paramylum and starch) for oil and leucosin; the elaboration of the outer protoplasmic layer into a firm periplast and finally into a definite membrane (in some cases consisting of cellulose) which may form either a close-fitting or an outstanding and cup-like perisarc; the outgrowth of tentacles from the periplast; and the development of sculpturings and of various excrescences (ridges, spines, etc.) on the cell-wall.

The Chromulinales include the simplest forms of the Chrysomonadineæ. In the lowest family, Chrysapsidaceæ, the cells are free-living and are amœboid; in *Chrysapsis* the chromatophore is an indefinite reticulate peripheral sheet, while in *Chrysamœba* and *Nannochrysis* it is basin-shaped, though in some species of *Chrys-*

amœba it becomes deeply bilobed and even divided into two (Fig. 5, *1*, *2*). In *Chrysapsis*, division often occurs within a gelatinous investment, while in *Nannochrysis* the formation of a palmella-stage is more pronounced and several divisions occur before the products of division become free by dissolution of the jelly. These simple forms show marked resemblance to some of the simpler Protomastigineæ; *Chrysamœba* is very similar to *Mastigamœba* and *Oikomonas*, apart from the absence of a chromatophore in the latter genera.

The Chromulinaceæ, forming the largest family of Chromulinales, include solitary and colonial forms, the former showing a elaboration of the protoplast as compared with the Chrysapsidaceæ; there is usually a single basin-shaped chromatophore, but sometimes two or even more may be present. Among the solitary forms, *Chrysococcus* (Fig. 5, *15*, *18*) has a thick shell or perisarc closely investing the periplast, but with a small anterior opening for the flagellum, the periplast of some species is ornamented with wart-like out-growths, and there is either a basin-shaped chromatophore or two lateral curved plate-like chromatophores, or several discoid chromatophores (Pascher, 99). A further elaboration is seen in the curious epiphytic genera *Chrysopyxis* and *Stylococcus*, in which the body is amœboid and lies freely within a goblet-like shell or perisarc which projects freely beyond it, and is produced at the base into a hapteron; longitudinal division occurs within the shell, and one of the daughter-cells escapes, produces a perisarc with an attaching process, and settles down; the cell contains cellulose, and the "flagellum" is in reality a "rhizopodium," or branched filamentous pseudopodium, at any rate in *Chryopyxis* (Fig. 5, *26-30*), which may be regarded as practically a *Chrysamœba* that has become epiphytic and produced a shell; in *Stylococcus* (Fig. 5, *23-25*), the "flagellum" is unbranched, but differs from the normal type of flagellum in being motionless and is doubtless pseudopodial.

The colonial genera of Chromulinaceæ show an advance upon the Chrysapsidaceæ, in that the palmella stage is more enduring, and in the genus *Hydrurus* becomes dominant. In *Chromulina Hokeana*, division occurs in the motile state, and the products of two or three successive divisions remain coherent to form a four- or eight-celled motile colony, comparable with the cœnobia of *Gonium* and *Pandorina*, and thus representing the "Volvocine tendency" which has appeared independently in several distinct groups of Chrysomonads. In most species of *Chromulina* (Fig. 5, *9-14*). however, division occurs in a resting palmella state (after the cells have lost their flagellum), giving rise to an indefinite mucilaginous mass; the free flagellate cells are amœboid and resemble *Chrysamœba*. A far more enduring and definite palmella state occurs in *Hydrurus* (Fig. 5, *37–41*); the motile cells ("zoogonidia") are of tetrahedral form, with the flagellum at the broader anterior end and on coming to rest lose the flagellum, become attached assume an ellipsoid form, secrete a mucilaginous stalk, and by repeated division give rise to an elaborately and regularly brancbed colony of considerable size. In this colony the cells are more crowded in the smaller branches than in the main axis and the larger branches; the whole structure behaves like a multicellular plant, growth in length depends on single apical cells, and the zoogonidia are produced from the branches, two or four arising by division of a parent-cell.

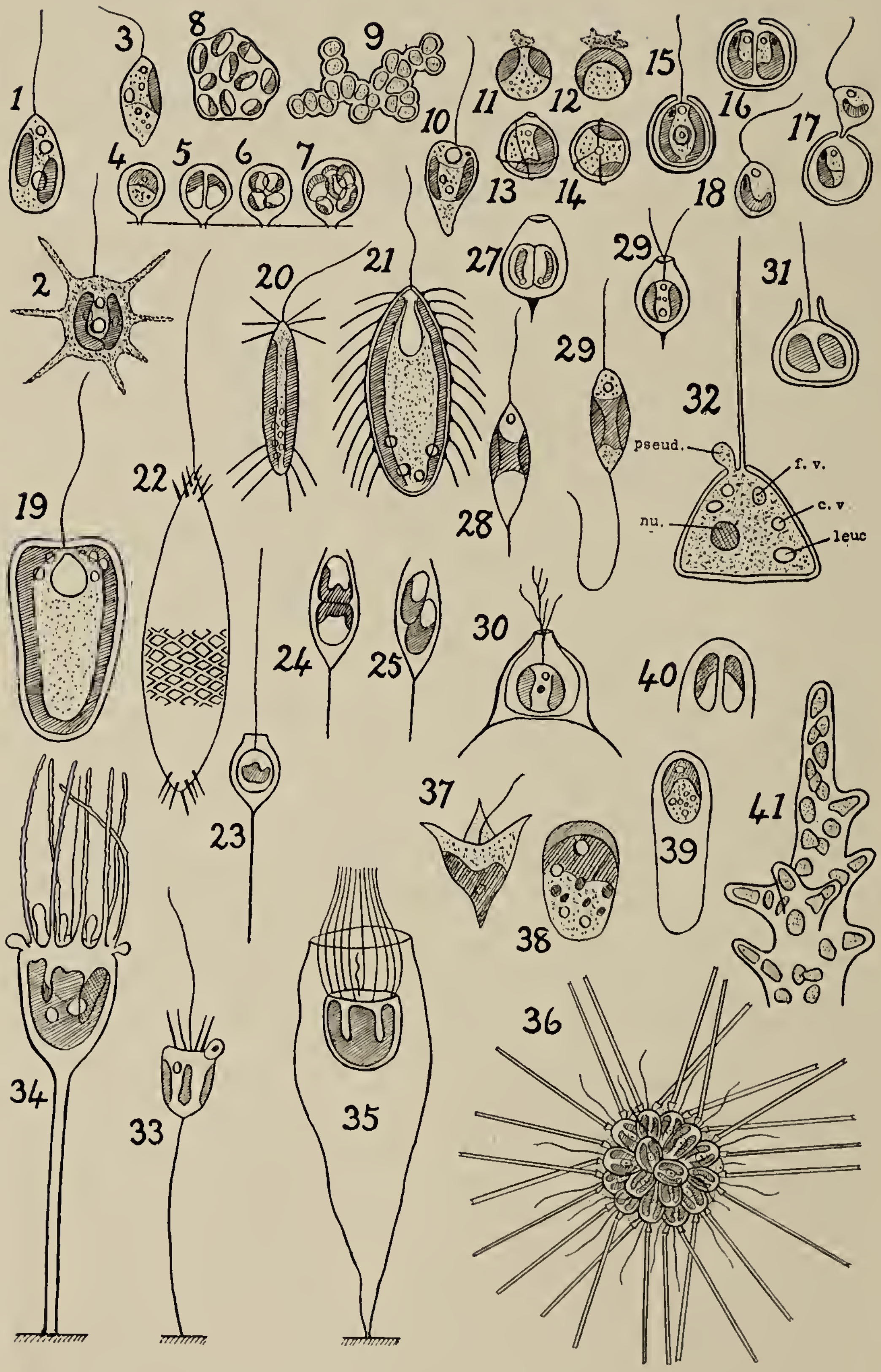

Fig. 5. CHROMULINALES.—1 and 2, *Chrysamœba radians* Klebs: 1, a normal free swimming individual; 2, an amœboid form. 3 to 9, *Chromulina Rosanoffii* (Woronin) Bütschli: 3, motile cell or zoogonidium; 4 to 7, division of a motionless encysted cell floating on the surface of the water; 8 and 9, formation of palmella stage. 10, *Chromulina ovalis* Klebs, motile cell. 11 to 14. *Chromulina nebulosa* Cienk., showing development of cyst; in 11 and 12, a portion

of the protoplasm is extruded from a pore, this amœboid mass being used up in the formation of the cyst membrane; 13 and 14 are different views of the fully formed cyst. 15 to 18, *Chrysococcus rufescens* Klebs: 15, a motile cell, in optical section, showing projection of the flagellum through a pore in the thick perisarc; 16, division of the protoplast; 17, escape of a daughter-cell; 18, free daughter-cell, before formation of perisarc. 19, *Microglena punctifera* Ehrb., showing the vacuole system. 20, *Mallomonas litomesa* Stokes, with flinty processes at anterior and posterior ends of the cell, 21, *Mallomonas acaroides* Ehrb., with similar processes nearly covering the cell. 22, *Mallomonas pulcherrima* Stokes, showing in part the reticulate sculpture of the perisarc. 23 to 25, *Stylococcus aureus* Chodat: two stages of division in 24 and 25. 26 to 30, *Chrysopyxis bipes* Stein: in 26 the flagellum is forked; 27 shows longitudinal division into two daughter-cells; 28 and 29, a daughter-cell with elongating posterior process for attachment—in 30 this process has wound around a *Zygnema* filament, part of which is seen in transverse section at the base of the sessile flask-like perisarc. 31, *Lagynion Scherffeli* Pascher. 32, *Heterolagynion Oedogonii* Pascher: to the left of the stout motionless flagellum is a short blunt pseudopodium *(pseud.)*; within the stout perisarc the protoplasm contains a nucleus *(nu.)*, a food vacuole *(f.v.)*, two contractile vacuoles *(c.v.)*, and two leucosin masses *(leuc.)* 33, *Pedinella hexacostata* Wys., with four stiff bristles at the base of the flagellum; on the right is an amœboid pseudopodium containing a food vacuole. 34, *Cyrtophora pedicellata* Pascher, showing the central flagellum, the stout nodulose tentacles, and several pseudopodial processes at the anterior end of the protoplast. 35, *Palatinella cyrtophora* Laut., with short flagellum in the centre of the ring of tentacles. 36, *Chrysosphærella longispina* Laut., a motile cœnobium of *Chromulina*-like cells, each with two long flinty processes exserted from cup-like outgrowths of the periplast. 37 to 41, *Hydrurus fœtidus* (Vauch.) Kirchner: 37, a motile cell or zoogonidium; 38, motionless cell, which becomes attached by a gelatinous stalk (39) and by division (39) gives rise to the branching colony, a portion of which is shown in 41.

1, 2, 10, 15 to 19, 21, 37 to 40, from Klebs; 3 to 9, from Woronin; 11 to 14, from Cienkowsky; 20, 22, from Stokes; 23 to 25, from Chodat; 26 to 30, from Stein; 31, 32, 34, from Pascher; 33, from Wysotzki; 35, 36, from Lauterborn; 41, from Berthold.

Hydrurus and other palmelloid Chrysomonads have been regarded by some writers as belonging to the Phæophyaceæ, on account of the dominance of the palmella stage in the life history, but apart from the fact that various degrees of elaboration of this stage have been observed in undoubted Flagellates, the terminal insertion of the flagella in the lower Chrysomonads, as compared with the characteristic lateral flagella of the Brown Algæ, seems to form an insuperable obstacle to the derivation of the Phæophyceæ from these Chrysomonads. Despite the dominance and elaboration of its palmella stage, *Hydrurus* can hardly be said to have crossed the "border-line" between Flagellates and Algæ; it is simply a Flagellate, allied closely to the lower Chrysomonads, and represents the culmination of a line of palmelloid forms arising from types like *Chrysapsis* and *Nannochrysis*. The "Volvocine tendency" shown in *Chromulina Hokeana* is carried further in *Chrysostephanosphæra*, recently discovered by Scherffel; here the cœnobium consists of sixteen cells arranged as in *Stephanosphæra* on the equator of a globular gelatinous mass, but later a palmelloid state is produced in which each cell has its own mucilaginous envelope.

Further elaboration in the external and internal characters of the cell is seen in the small family of Mallomonadaceæ, consisting of the two free-living genera *Mallomonas* and *Microglena* and the colonial genus *Chrysosphærella*. In *Mallomonas* (Fig. 5, *20-22*) the ovoid or elongated cell has a close-fitting shell composed of tesselated polygonal plates, and either each plate, or only those at the two ends of the body, may bear fine silicified outgrowths; there are two chromatophores, and the hinder end of the cell contains numerous contratile vacuoles, while at the anterior end there is a large non-contractile vacuole; the cysts are also covered with a silicified shell. In *Microglena* (Fig. 5, *19*) the vacuole system is further elaborated, all the vacuoles being anterior, the smaller contractile vacuoles surrounding a large non-contractile vacuole; there is frequently a single basin-like chromatophore; the shell is thin and bears only scattered granular outgrowths. In *Chrysosphærella* (Fig. 5, *36*) the cells are united by their hinder ends in a spherical jelly, forming a motile *Pandorina*-like cœnobium; each cell bears on its free outer (anterior) end two small cup-like outgrowths from the shell (which has the same structure as in *Mallomonas*) and from each of these cups there springs a long flinty spicule; the internal structure of the cells resembles that of *Microglena*, there are two chromatophores, each with a stigma.

Pascher (102) has founded a fourth family of Chromulinales, the Cyrtophoraceæ, upon three very remarkable epiphytic genera which have probably arisen from a type like *Chrysopyxis*. These genera—*Pedinella*, *Palatinella*, *Cyrtophora* (Fig. 5, *33-35*)—are either sessile or stalked, the body is flattened anteriorly and bears a central flagellum surrounded by from six to twenty pseudopodia; there is a single basin-shaped chromatophore, but this is more or less deeply lobed in front. Pascher (109) has recently described a genus (*Lagynion*) which forms a transition between *Chrysopyxis* and the Crytophoraceæ; in *Lagynion* (Fig. 5, *31*) the cell is fixed by a broad base, and within the collar-like projecting portion of the shell the protoplast protrudes short amœboid pseudopodia around the base of the long motionless flagellum or "rhizopodium." The same writer describes a colourless genus, *Heterolagynion* (Fig. 5, *32*,) evidently derived from *Lagynion*, and points out that the Cyrtophoraceæ show a remarkable parallelism with the Pantostomatinean genera *Pteridomonas* and *Actinomonas*.

In the Isochrysidales the cells are either free-living or united to form colonies of the Volvocine type. Of the nine genera placed here (as Hymenomonadaceæ) by Senn, the unicellular genus *Wysotzkia* should be transferred to the Phæochrysidales (Cryptomonads), and the palmelloid genera *Phæocystis* (Ostenfeld 96), and *Nægeliella* (Correns, 27) to the Phæocapsaceæ; in these three genera the two flagella are inserted laterally, and while *Wysotzkia* is clearly related to the simpler Cryptomonads, especially to the two recently discovered genera *Protochrysis* and *Cryptochrysis*, it seems equally obvious that the affinities of *Phæocystis* and *Nægeliella* are with the lower Phæophyceæ, hence they should be removed from the Brown Flagellata altogether. In the simplest Isochrysid genus, *Hymenomonas* (Fig. 6, *1*), the cell has a firm thick periplast, though the anterior portion of the protoplast is naked and capable of putting forth pseudopodia. In this order, evolution appears to have taken place in two directions, one leading to epiphytic forms recalling *Chrysopyxis* and its allies among the Chromulinales, the other to motile colonies. Of the epiphytic forms, *Stylochrysalis* (Fig. 6, *3*), is attached to its substratum (usually an *Eudorina* colony), by a long stalk dilated at the base, and has a thin periplast; while *Derepyxis* (Fig. 6, *2*) resembles *Chrysopyxis* in having an outstanding perisarc with a projecting collar. Of the colonial forms, *Syncrypta* and *Synura* have globose motile cœnobia, consisting of 16 to 64 biflagellate individuals closely aggregated in a radial manner, their pointed hinder ends directed towards the centre of the cœnobium; in *Syncrypta* (Fig. 6, *6*) the cells have a thin periplast and the

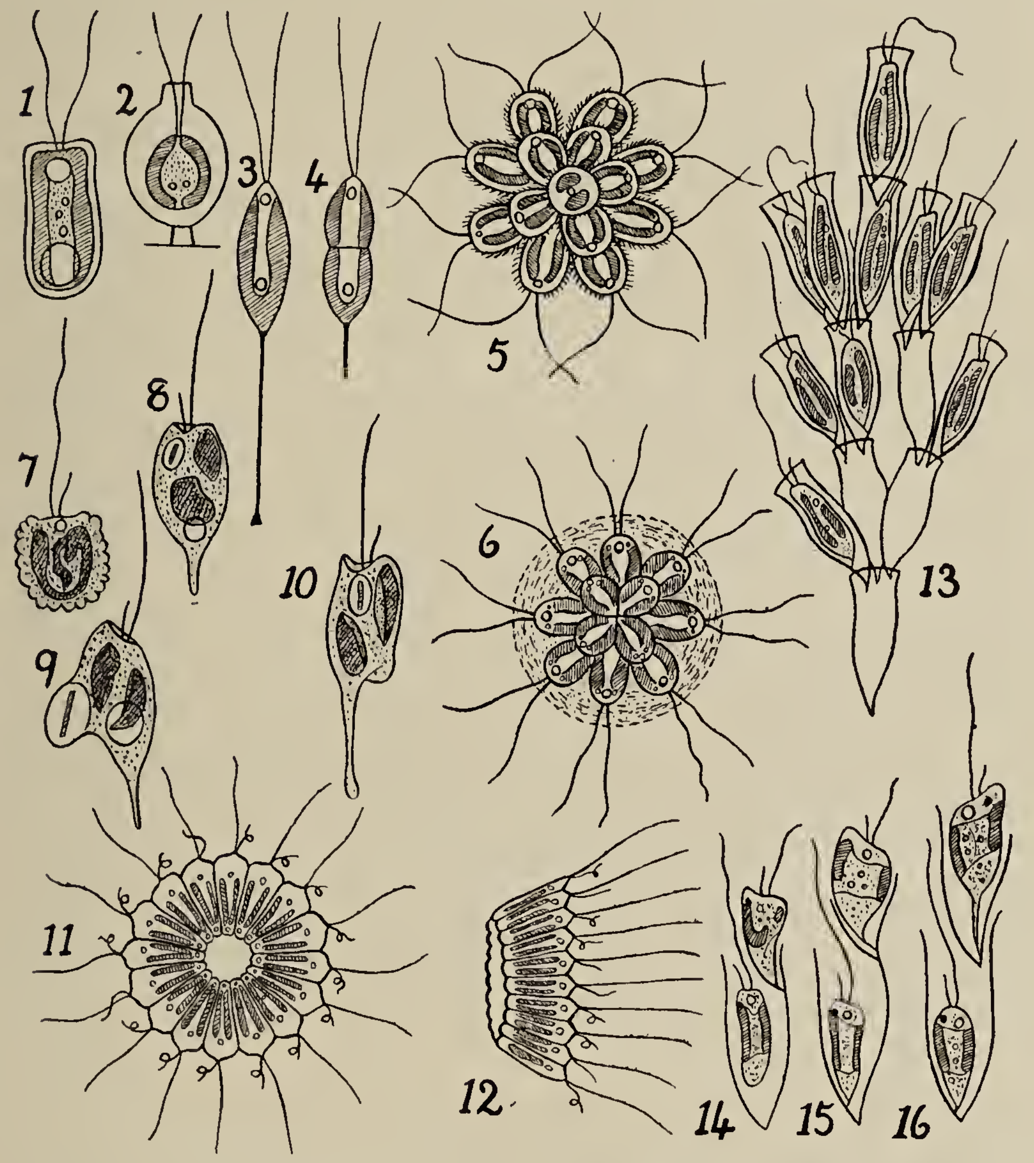

Fig. 6. Isochrysidales (1 to 6) and Ochromonadales (7 to 16).—1, *Hymenomonas roseola* Stein. 2, *Derepyxis dispar* Stokes. 3, *Stylochrysalis parasitica* Stein (in 4, transverse division is shown). 5, *Synura Uvella* Erhb. 6, *Syncrypta Volvox* Erhb. 7, *Ochromonas crenata* Klebs. 8 to 10, *Ochromonas mutabilis* Klebs, showing migration of food vacuoles within the protoplasm and amœboid changes of form of the cell. 11, 12, *Cyclonexis annularis* Stokes: in 11 the cœnobium is seen from the surface, in 12 from the side. 13 to 16, *Dinobryon Sertularia* Ehrb.: in 14 to 16, stages in division and perisarc formation.

1, from Klebs; 2, 11, 12, from Stokes; 3 to 6, from Stein; 7 to 10, 14 to 16, from Klebs; 13, from Senn.

colony is invested in mucilage through which the flagella protrude, in *Synura* (Fig. 6, *5*) there is no mucilaginous covering and each cell of the colony has a firm periplast beset with spines or warty outgrowths—in *S. Klebsiana* each cell bears two flinty spicules, as in *Chrysosphærella.* Pascher (110) has observed that in *Synura uvella* the contents of a cell may escape as an amœba instead of a flagellate swarmer, and that the latter may also become amœboid after liberation, and that from both flagellate and amœboid forms palmella-states may arise by division in a mucilaginous motionless condition (Conrad, 26).

The Ochromonadales, though a smaller order than the Chromulinales and Isochrysidales, shows parallel developments of the same kind. Here again we begin with a unicellular and potentially amœboid type, *Ochromonas* (Fig. 6, *7-10*), which, except in having two unequal flagella, closely resembles *Chrysamœba* among the Chromulinales; most of the species are free-swimming, but *O. tenera* becomes fixed by its hinder end; the thin periplast is capable of secreting mucilage, and in *O. socia* division occurs in the motile phase and gives rise to small, generally four-celled, motile cœnobia; usually, division occurs in a resting state, and in *O. botrys* a large mass of cells enveloped in mucilage may be formed in this way. In *Cyclonexis* (Fig. 6, *11*, *12*), the individual cells are like those of *Ochromonas*, but they remain in lateral contact in such a manner as to form a radiating ring-like cœnobium, consisting usually of 16 cells. In *Uroglena* a curious type of cœnobium is formed as the result of repeated division of the stalked cells and the formation of a spherical mucilage mass in which the cells lie near the periphery while the branching stalks radiate from the centre. In *Dinobryon* (Fig. 6, *13-16*) the cell is spindle-shaped and is invested loosely by a vase-like shell widely open above; when division occurs, the daughter cells may either escape or (in most species) become attached to the mouth of the shell and produce a shell of their own; by repetition of this process, a branching colony is built up; the shell in some cases gives cellulose reactions. The genus *Dinobryon* has been monographed by Brunnthaler (16) and by Lemmermann (79).

VII.—The Cryptomonads and their Relationships.

It would appear that the three orders of Chrysomonadineæ dealt with thus far (Chromulinales, Isochrysidales, Ochromonadales) have not given rise to anything higher than a Flagellate, though they show various attempts at the formation of colonies —in all three orders we find gradual elaboration of motile "Volvocine" cœnobia, and also the working out of a palmelloid or "Tetrasporine" tendency towards the formation and dominance of a non-motile multicellular vegetative condition. It may be noted that "Volvocine" cœnobia occur also among the Protomastigineæ (*Protospongia*, *Sphærœca*, etc.), in addition to the dendroid colonies of the *Dinobryon* type (*Codonocladium*, *Salpingœca*, etc.) derived from solitary "choanflagellate" forms (*i.e.*, forms with outstanding collar-bearing perisarc). Whether the remarkable resemblances between the "mastigamœboid," the "Volvocine," and the solitary and dendroid "choanoflagellate" types met with in the colourless Pantostomatineæ and Protomastigineæ on one hand and the Chrysomonadineæ on the other are to be interpreted as examples of parallel developments, or whether, as suggested by Pascher and Scherffel, they indicate derivation of part at any rate of the colourless Flagellate families from Chrysomonads, the trend of recent work on the Brown Flagellata is decidedly against the view that the Chrysomonads comprised in families Chromulinales, Isochrysidales, and Ochromonadales have given rise to the Brown Algæ.

The case appears to be quite different with the fourth Chrysomonad order, the Phæochrysidales or Cryptomonads, which are distinguished by the *lateral* insertion of the two flagella. The simplest forms are Pascher's new genera *Cryptochrysis* and *Protochrysis* (103); *Wysotzkia* (hitherto placed in the Isochrysidales); and *Nephroselmis* (Senn, 136), which Wille (150) includes in the Volvocaceæ. Senn (135) defines the Cryptomonads as having an ovoid and flattened body, with two equal flagella arising just behind the anterior end from a groove which is continued into a gullet-like cavity, and having one or two contractile vacuoles which are not coördinated into a pulsating system. According to Senn they are also further differentiated from the Chrysomonads by producing starch, or, at any rate, a refractive solid carbohydrate. The researches of Pascher and others have shown, however, that the Cryptomonads, though a highly specialised group, cannot be set apart from the Chrysomonads, as a separate group of the Flagellata, and that they have arisen from the Chrysomonads by further internal differention of the protoplast, accompanied by a shifting of the flagella from a terminal to a lateral position. In *Wysotzkia* (Fig. 7, *3*, *4*), the posterior end of the protoplast, behind the two chromatophores, is naked and capable of amœboid movement. In *Cryptochrysis* (Fig. 7, *2*), the lateral insertion of the flagella is more marked than in *Wysotzkia*, the flagella arising from a deep longitudinal groove which is about half the length of the body and is covered with minute granules; nutrition is purely holophytic and the assimilate consists of disc-like grains giving a reddish violet colour with iodine; division takes place in the motile state, and is longitudinal.

Cryptochrysis appears to be the most primitive Cryptomonad at present known; *Wysotzkia*, though simpler in some respects, undergoes transverse division, and is adapted for partial or facultative holozoic nutrition. *Nephroselmis* and *Protochrysis* differ from these genera, and indeed from the remaining Cryptomonads, in that the groove is transverse and occupies the middle of the protoplast, so that the flagella arise from the middle of the concave side of the body; in *Nephroselmis* there is a single chromatophore which follows the outline of the body and is interrupted only at the point of emergence of the flagella, and division occurs in the motile condition, whereas in *Protochrysis* (Fig. 7, *1*), there are two chromatophores, and division occurs after the cells have become rounded off and invested in mucilage, a four- or eight-celled colony being formed by repeated division in this palmella-state. In *Cryptomonas* (Fig. 7, *5*—*7*), the groove found in the genera just mentioned is replaced by a canal which leads into the interior of the protoplast; in some species this canal is quite short, in others it extends for about half the length of the body. In most species of *Cryptomonas* the assimilate is like that found in *Crypto-*

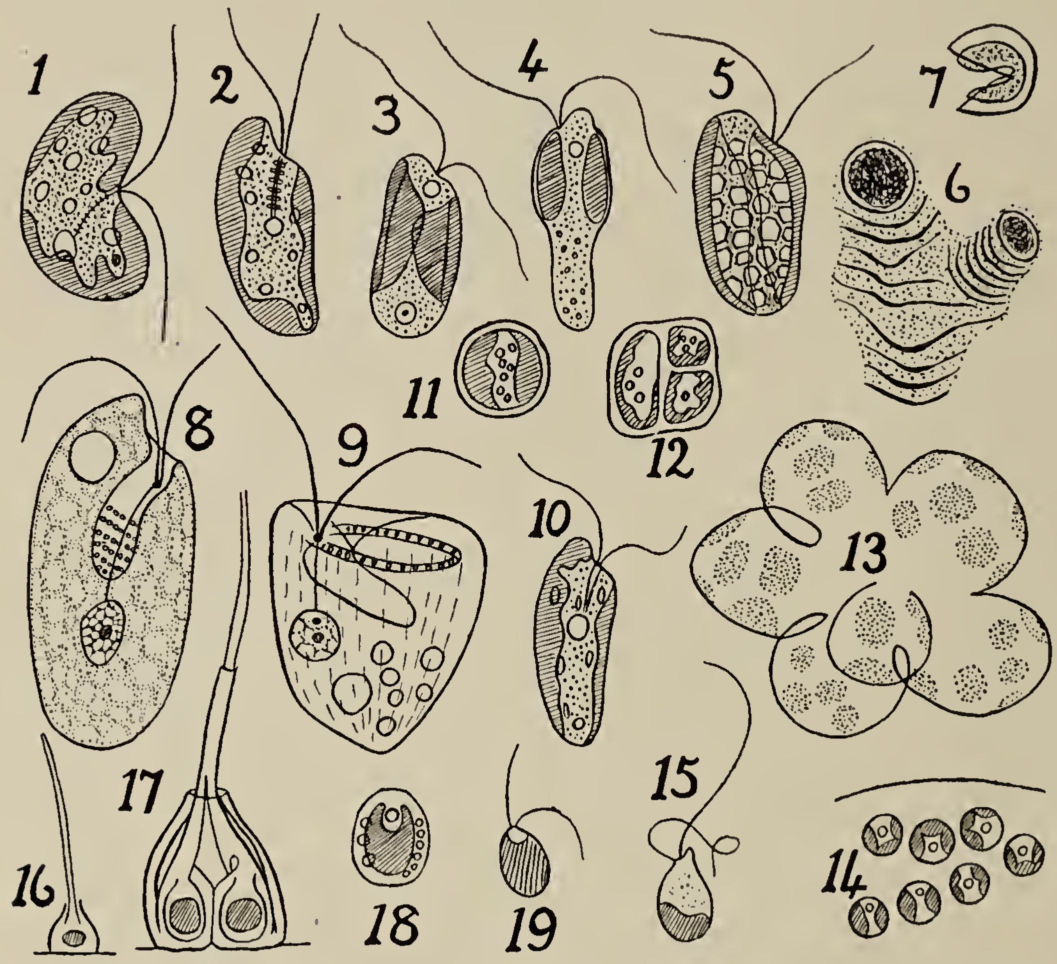

Fig. 7. Cryptomonads (1 to 9) and Phæocapsaceæ (10 to 19) :—1, *Protochrysis phæophycearum* Pascher. 2, *Cryptochrysis commutata* Pascher. 3, 4, *Wysotzkia biciliata* (Wys.) Lemmerm. : 3, ordinary form ; 4, metabolic (amœboid) form, showing protrusion of pseudopodia anteriorly and posteriorly. 5 to 7, *Cryptomonas erosa* Ehrb. : 5, ordinary motile cell ; 6, two encysted cells with gelatinous envelopes ; 7, ruptured cyst membrane. 8, *Chilomonas Paramæcium* Ehrb. : the flagella arise on the ventral side of the "gullet" (which shows several circles of granular markings in its lower half), from a small body which is connected with the nucleus by means of a long fibril. 9, *Cyathomonas truncata* (From.) Fresen. : structure essentially as in *Chilomonas* ; there are numerous food vacuoles at the base of the cell, the single contractile vacuole is seen near the opening of the "gullet." 10 to 12, *Phæoplax marina* (Reinisch) Pascher : 10, motile cell ; 11 and 12, young colonies (beginning of palmella stage, which when fully developed resembles that seen in *Chromulina Rosanoffii*, Fig. 5, *9*). 13 to 15, *Phæocystis Poucheti* Lagerh. : 13, gelatious colony (palmella state) ; 14, a portion of same, more highly magnified) ; 15, a motile cell (zoogonidium). 16 to 19, *Nægeliella flagellifera* Correns : 11 and 12, one-celled and three-celled stages in development of colony, showing the perisarc and bristles ; 18, a single cell, showing the bell-shaped chromatophores ; 19 a motile cell (zoogonidium).

1, 2, from Pascher ; 3, 4, from Wysotzki ; 5 to 7, from Senn ; 8, 9, from Ulehla (with some details inserted from Hartmann and Chagos) ; 10 to 12, from Reinisch ; 13, 14, from Lagerheim ; 15, from Pouchet ; 16 to 19, from Correns.

chrysis, but in *C. ovata* starch is produced; longitudinal division may occur in either the motile or the encysted condition, and the cyst membrane gives the reactions of the cellulose. *Chroomonas* and *Cyanomonas* resemble *Cryptomonas*, but the chromatophores are blue-green, while *Rhodomonas* is allied to these forms but has a red chromatophore. *Chilomonas* (Fig. 7, *8*) also resembles *Cryptomonas* in structure, but is saprophytic, though it produces starch; *Botryomonas* (Schmidle, 131) is another saprophytic starch-producing form, in which the cells become aggregated to build up a branched gelatinous colony, and the periplast gives cellulose reactions. *Cythomonas* (Ulehla, 143) and *Oxyrrhis* (Senn, 136), though placed by Senn in the Protomastigineæ, are apparently related closely to *Cryptomonas* through *Chilomonas*, and may be regarded as colourless forms derived from a *Cryptomonas*-like type; in *Cyathomonas* (Fig. 7, *9*) nutrition is mainly saprophytic, but solid food can also be ingested at the anterior end of the body, while in *Oxyrrhis* nutrition is mainly holozoic and this genus differs from its allies in undergoing transverse division.

The Cryptomonads have probably arisen from simple Chrysomonads, with two flagella either of unequal length or with different orientation (one directed forwards and the other backwards in swimming). Such a form as *Ochromonas*, for instance, may well have given rise to the Chloromonadineæ on one hand and to the Cryptomonads on the other, for these two groups show somewhat striking parallelisms, such as the organisation of the vacuole system into small actively contractile vacuoles which open into a large anterior non-contractile vacuole or into a groove or canal. The Chloromonads have probably given rise on one hand to the highly differentiated Eugleninеæ which have no Algal affinities, and on the other to the Algal group "Confervales" (Heterokontæ). Similarly the simpler Cryptomonads—e.g., *Cryptochrysis* and *Protochrysis*—appear to have given rise on one hand to highly organised Flagellates like *Cryptomonas*, *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*—corresponding to the Eugleninеæ in the green series—and on the other to the Phæocapsaceæ, which form the starting-point of the Brown Algæ.

The Phæocapsaceæ, corresponding roughly with the Tetrasporaceæ and Palmellaceæ in the green series, are apparently a somewhat heterogenous group, marked by the dominance of the non-motile phase. One of the simplest genera is *Phæocystis* (Fig. 7, *13-15*) in which the cells have from one to four plate-like chromatophores and are aggregated to form a rounded gelatinous colony, the motionless cells being rounded, while the motile cells ("zoogonidia") are biflagellate and have the same structure as *Wysotzkia* (Lagerheim, 73; Ostenfeld, 96; Scherffel, 122). In a similar form described by Reinisch (120) as *Phæococcus marinus* (Fig. 7, *10-12*) but regarded by Pascher (104) as the type of a new genus, *Phæoplax*, the motile cells correspond closely to *Cryptochrysis*. *Phæococcus Clementi* is a gelatinous form adapted to subaërial life, the cells having firm envelopes, and the motile cells show typical Cryptomonad structure; whether *P. paludosa* described by West (146) belongs to this genus, or indeed to the Phæocapsaceæ, is somewhat doubtful, since in his figures the motile cells resemble those of the Isochrysidal Chrysomonads and not the Cryptomonads.

The position of *Phæosphæra* West is also doubtful, as the motile cells have apparently not yet been observed; the same is the case with *Stichoglœa* and *Gleothamnion*, which would be included in the Phæocapsaceæ if their motile cells were found to show Cryptomonad characters. *Nægeliella* is epiphytic and forms multicellular discs, the individual cells producing a perisarc prolonged into a bristle; the motile cells have a single brown chromatophore and two laterally inserted flagella. The genus *Phæothamnion* appears to represent the highest form of the Phæocapsaceæ, while *Pleurocladia* leads directly to the Ectocarpaceæ and is placed in that group by Kjellman and Svedelius (66). A useful bibliography of the genus *Phæothamnion* is given by M'Keever (91), who recently discovered *P. confervicolum* (the only species known) in Scotland—it was previously recorded only from Sweden, Germany and Italy. There appears to be some doubt as to the insertion of the flagella and the nature of the motile cells; according to Lagerheim the latter are zoogonidia with terminal flagella and no eye-spot, while Borzi described the conjugation of isogamous gametes with lateral flagella and a red stigma. Oltmanns (95) places *Phæothamnion*, with the other genera here regarded as forming the family Phæocapsaceæ, among the Chrysomonadineæ. This genus is, however, apparently related very closely to *Pleurocladia*, which has the typical gonidangia and gametangia of the Ectocarpaceæ. Bohlin's genus *Phæodactylon* (9) cannot be included in the Phæocapsaceæ, but is probably a Chrysomonad in which adaptation to plankton conditions has resulted in loss of the flagella; its curious three-armed cell recalls the tetrahedal motile cells of *Hydrurus*.

The greatest difficulty in the way of deriving the Phæophyceæ from the Brown Flagellates has been the characteristic lateral insertion of the flagella in the motile cells of the Brown Algæ—excepting in the Dictyotaceæ, which are somewhat isolated among the Phæophyceaæ. This difficulty has, however, been overcome by the discovery of *Protochrysis*, in which the furrow from which the flagella arise, instead of being longitudinal and subapical as in other Cryptomonads, is transverse, so that the flagella arise from the middle of the body, one flagellum being directed forwards and the other backwards. *Protochrysis* appears to stand very near the ancestral type which gave rise to the lower Phæophyceæ or to the series of transitional forms (Phæocapsaceæ) leading through *Phaeothamnion* and *Pleurocladia* to the Ectocarpaceæ.

The work of Pascher and Scherffel supports Klebs' view that the Cryptomonads have arisen from the Chrysomonads and have no direct relationships with any other Flagellate group excepting possibly the Dinoflagellata (Peridiniales). Pascher, as we have already seen, merges the Cryptomonads in the order Chrysomonadineæ, and has shown that the organisation of a pulsating vacuole system, previously regarded as found only in the Chloromonads and the Euglenineæ, occurs not only in the Cryptomonads but also among the Chrysomonad groups. Another distinction made by previous writers between the Cryptomonads and Chrysomonads has broken down, namely, that relating to the nature of the assimilation products. According to Senn, the Chrysomonads produce oil and leucosin, and nutrition may be holozoic or saprophytic or holophytic, while in the Cryptomonads starch is produced and nutrition is never holozoic. Pascher has shown, however, that although starch is formed in certain Cryptomonads (*Cryptomonas erosa*, *Chroomonas baltica*, *Chrysidella*, *Chilomonas*), this is not the case in other forms which have been investigated (*Protochrysis*, *Cryptochrysis*, *Chroomonas Nordstedtii*) nor in the Phæocapascæ, where the assimilate is either leucosin or oil. All that can be said on this head is that solid assimilation products are relatively rare in the Chrysomonads and relatively common in the Cryptomonads. Again, the beginnings of the characteristic furrow of the Cryptomonads are seen in the Ochromonadales, and even in the Chromulinales, where the anterior end of the body shows a pit in which the flagellum is inserted.

(*To be continued*).

LABORATORY NOTES.

METHOD OF DOUBLE-STAINING MICROTOMED SECTIONS IN THE RIBBON.

In the course of an investigation on the anatomy of the rhizome of *Statice Limonium*, considerable difficulty was experienced owing to the fact that though the tissues embedded well in paraffin, and cut easily, immersion in xylol for the removal of the wax immediately washed the sections from the slide This was probably due to the fact that the periphery of the sections is occupied by a well developed cork layer which adheres imperfectly to the slide (although the egg-albumen was known to be in good condition), and tends to separate from it even during the drying process following on the floating-out of the ribbon in water. As it was necessary to obtain serial sections, various experiments were tried based on the methods described by T. G. Hill,[1] and the following are the chief results obtained.

METHOD I. *Sections which show a tendency to wash off the slide.* e.g., *Statice Limonium* rhizome.

The ribbon is floated out on the prepared slip with Delafield's Haematoxylin,[2] the slip is warmed until the sections are quite flat and the superfluous stain is then drained back into the bottle. The Hæmatoxylin is replaced by a saturated solution of Safranin in 50% alcohol, care being taken that the stain flows under the ribbon and not over it; after a few minutes the stain is drained off, the sections are "blotted down" with hard smooth blotting paper, and the slide is allowed to dry either by exposure to air or by warming. The preparation is completed, *without removal of the paraffin*, by mounting in rather liquid canada balsam.

If a single stain is sufficient, either Safranin or Gentian Violet gives excellent results, since the tissues are stained generally.

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[1] A method of Staining Microtomed Sections in the Ribbon. New Phyt. Vol. xi, No. 2, Feb. 1912.

[2] Ehrlich's Hæmatoxylin gives very poor results, and Mr. Hill informed me that this was the formula he used.

It might be supposed that mounting in the paraffin in this way would tend to obscure the tissues through the staining of the paraffin itself. If, however, the excess of stain is drained off thoroughly and the sections gently pressed down with blotting paper, very clean preparations are obtained, the wax being stained hardly appreciably. If the slides are warmed after mounting, the rather liquid canada balsam (in xylol) dissolves the wax almost entirely, if not quite.

If the sections do not shew a tendency to wash off the slide, the following method is preferable.

METHOD II. *Sections which adhere to the slide and do not wash off.*

The process described under Method I is followed as far as the "blotting down" of the ribbon. The slide is then gently warmed until the paraffin has melted and the wax is removed by treatment with xylol. If necessary the staining can be controlled at this stage by rinsing in absolute alcohol; clearing with xylol follows and the preparation is completed by mounting in canada balsam.

Equally good results are obtained in Method II by mixing the Hæmatoxylin and Safranin (equal parts) and floating the ribbon on the mixture, for any overstaining can be controlled by washing in absolute alcohol after removal of the wax.

Various other stains have been tried, with the following results:

1. A saturated solution of Safranin in 50% alcohol, followed by a satsrated solution of Lichtgrün in clove oil gives exceptionally good preparations for details of structure, For example, in a transverse section of the root of *Cephalotaxus* stained in this way, the thickenings on the walls of the *assise de soutien* are stained red, the cell-walls greenish red, and the protoplasmic lining to the cells bright green.

2. An alcoholic solution of Safranin followed by Methyl Green gives fairly good differentiation.

3. Methyl Green followed by Delafield's Hæmatoxylin is less satisfactory.

4. Gentian Violet followed by either Bismark Brown or Vesuvian Brown gives poor results.

The preparations made by these methods are quite as good as those obtained by the means commonly employed in double-staining processes. The methods have the great advantage that the whole process of double-staining and mounting a slide can be carried out in from 5 to 10 minutes hence the time-factor, which becomes of such importance in investigation, involving the anatomical examination of much material, becomes very considerably lessened by the double-staining of microtomed sections in the ribbon.

E. DE FRAINE.

UNIVERSITY COLLEGE, LONDON,
February 13th, 1913.

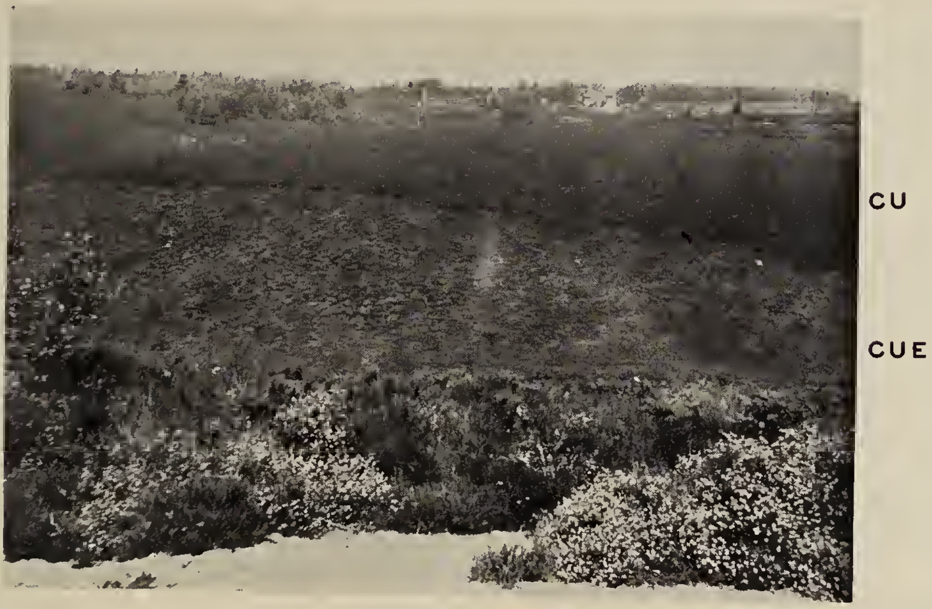

Fig. 1.

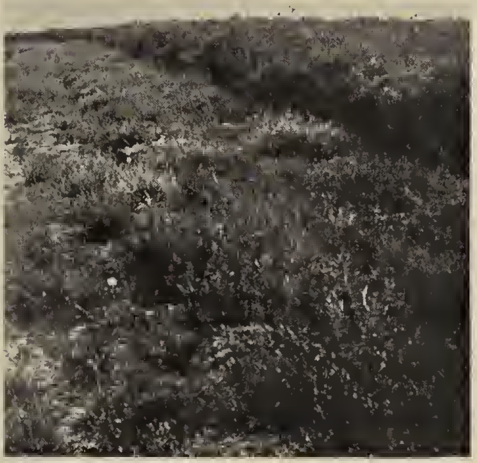

Fig. 2.

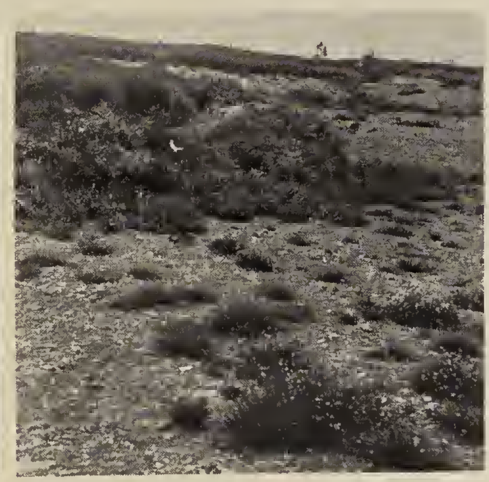

Fig. 3.

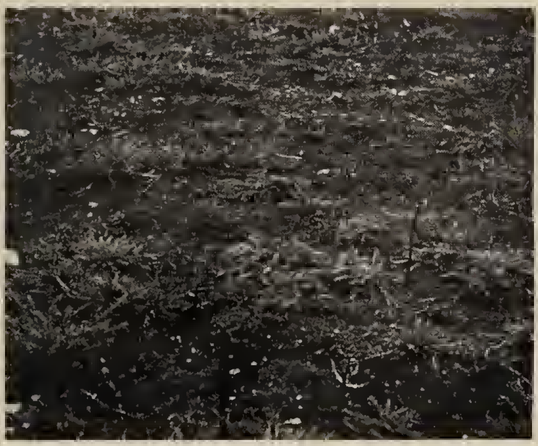

Fig. 4.

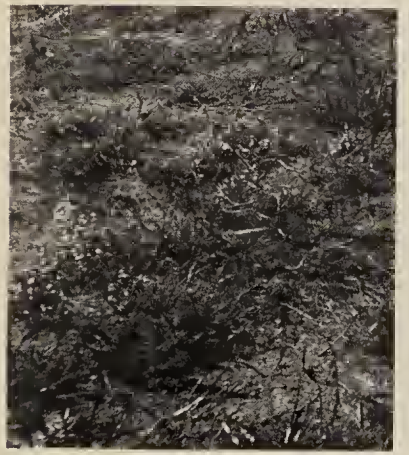

Fig. 5.

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THE COEFFICENT OF HUMIDITY: A NEW METHOD OF EXPRESSING THE SOIL MOISTURE.

BY W. B. CRUMP, M.A.,
Heath Grammar School, Halifax.

[WITH ONE FIGURE IN THE TEXT.]

I.—INTRODUCTION.

THE most obvious distinction between plant habitats is that based upon the quantity of water present and the permanence or fluctuation of the water supply. Such common descriptive terms as marsh, swamp, desert, or wet, boggy, dry, express this and serve to differentiate habitats in a general way. Proceeding further by deduction, field botanists are accustomed to estimate the comparative wetness of an area by the vegetation it supports, or by the presence of specific plants. But the development of ecology demands the replacement of these indefinite characters by more exact knowledge based upon quantitative analysis of the edaphic factors; knowledge of the magnitude of each that produces the static equilibrium revealed as a stable plant-association, and of the limiting values that determine the dynamic change from one association to another, or even the replacement of one formation by another. At present the nature of the master-factors that determine the existence of a formation is often a matter of supposition. Until a body of *data* has been accumulated it is impossible to know which of several possible factors controls the formation, or what is the magnitude of a given factor when it reaches its limiting value.

The importance of quantitative determinations of water-contents has been insisted on by F. E. Clements[1] and in laying stress on the water-content, and particularly the available water-content or chresard, as of more importance than the soil structure he has indicated a promising field for research in Ecology. But very little progress has been made in opening it out and this, apparently for two reasons. The direct determination of the available water-content in the field is impracticable under ordinary conditions, and when attempts have been made to determine the total water-content—the actual amount present as distinct from the maximum when the soil is saturated—the results have been discordant or inconclusive. So it comes about that whilst much attention has been given to soil physics and the relation between soil structure and water capacity, the particular information desired by the ecologist—the actual amount of water within the zone of root activities—is still non-existent. But the need of it is urgent. Even when definite soil types have been distinguished according to their chemical nature and physical structure and when the natural vegetation has been correlated with these types, the investigation is at least incomplete. To leave the water-content out of consideration is to omit the factor which links the two, the soil and the plant, together. Granted that the soil structure controls the water-content, still the latter may prove a much better index of the plant environment, either because it can be determined more simply, or expressed with greater precision, or because its relation to the plant is more direct and intimate. There may be cases where the nature of the soil is the controlling factor, but so long as the water-content is unknown its influence can neither be predicated nor denied.

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[1] "Research Methods in Ecology." Lincoln (Nebraska), 1905.

But it is necessary to consider at the outset whether it is possible to obtain a value for the water-content that will be in any way expressive of the habitat. Can it be regarded as a constant whose value for any given association may be determined by a series of analyses? How are the irregular fluctuations and the seasonal variation in the quantity of water present in the soil to be eliminated? Is it the mean value, or the maximum in the wet season, or the minimum in the dry season, that is the more significant? Is the range within such bounds as to afford a mean value that is in any way a criterion of the habitat? Experimental results afford an answer to such questions and soon show that the investigation of a plant-habitat does not admit of the rigorous measurement applicable in physics and chemistry. If the water-content of the *Calluna* habitat, for example, is a constant of nature it differs radically from an atomic weight and can never be stated with the same exactitude, for it is of necessity subject to considerable variation.

But variation from a specific type is axiomatic in biology and the determination of the mean or "mode" corresponding to the type has become a familiar problem in biometrics. Such a point of view is necessary in dealing with soils as plant-habitats. The number of veins in a beech leaf, as shown by Karl Pearson,[1] varies considerably, but by examining a large number of leaves a type, represented by the mode, can be established and the greatest number of individuals is aggregated round this mode. Beech leaves from another locality will possess an appreciably different mode and the range of variation will be extended by increasing the number of observations. But the extreme deviations from the mode will occur very rarely, in accordance with Galton's Law of Frequency.

Whether or no the water-content is the best method of expressing the soil-moisture may be left in abeyance for the moment. Whatever is selected as the criterion of the humidity of the habitat its values will show variation about a mean. If the deviations follow the normal curve of frequency, supposing a sufficient number of observations to have been made, the mean affords a definite index of the habitat, and a habitat that satisfies such a test is as much an entity as is a biological species. The extreme deviations will possess considerable significance, for they will indicate the physiological limits of the existence of the plant association. Above and below these limits the association can no longer exist and even before these points are reached it is likely to be invaded by members of other associations. Of the two, the minimum value probably has the greater significance for ecological purposes. If it is determined under such conditions as prevailed during the summer of 1911 it must give a close approximation to the true value of Clements' echard, or the non-available water in the soil, perhaps more so than values obtained "under control," or by cutting out blocks in the field.

II.—METHOD OF ANALYSIS.

Before proceeding to explain the method adopted for expressing the soil-moisture it is necessary to review briefly the process of analysis and the reduction of the results.

The soil sample taken within the layer of root activity is preserved in a tight tin. If in the laboratory it does not appear to be uniform it is divided into an upper and a lower layer and suitable blocks from the centre of each are rapidly weighed in tared porcelain dishes, after larger rootlets have been removed if present. These samples weigh from 15 to 60 grams, and the weight is determined within a centigram. They are then placed in a quiet room or airy cupboard and left to dry at about 15°C. until the weight is constant. This takes from one to three months. The loss of weight is the required water-content. The dishes are then heated in a water-oven (at 100°C.) until the weight is again practically constant. This further loss at 100°C. though recorded is *ignored* because it can be of no service to the plant. It includes hygroscopic moisture and water of combination and its value is tolerably uniform for the same type of soil so that it affords a check on the determination of the water lost at 15°C.

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[1] The Grammar of Science.

The dish and its contents are next subjected to a full red heat until all char has disappeared, and again weighed as soon as cold, or preferably placed in a desiccator to cool. The loss of weight is recorded as humus, as a more definite term than "loss on combustion" and quite in accordance with the use of the word humus to include all the decaying organic matter in the soil. The residue may consist entirely of vegetable ash, or may be almost wholly mineral in origin. If the soil is calcareous the lime must be reconverted into carbonate after combustion.

Such is the process of analysis. The percentage composition of the *wet* soil is then calculated from the results. But partly to conform to agricultural practice and partly because the wet soil represents no fixed standard, the values are then manipulated to express them in terms of 100 parts of *air-dry* soil, *i.e.*, of soil dried at 15°C. The water-content, otherwise the loss at 15°C., then becomes an *addition* to the 100 parts. Clearly, if a wet peat loses just 50% of its weight on drying in the air, the air-dry peat was "combined with" 100% of water. The principle is sound though it has disadvantages, for when the water-content is high originally it becomes much exaggerated in the final result. Even if agricultural analyses took note of the water lost on drying at 15°C. this disadvantage would not be apparent. But in the case of peats the statement of the water-content is paradoxical unless the exact expression receives careful attention, *e.g.*, "the water lost at 15°C. is 135% of the air-dry peat," means that there are 135 parts of water lost on every 100 parts of the air-dry peat that remains after drying. Slight differences are of course magnified in the same way, so that a variation of 1% in the water-content of a wet peat may become 50% in terms of the air-dry peat. The rapid increase in the higher terms is shown in the following table :—

WATER-CONTENT.

In terms of wet soil.	In terms of air-dry soil.
10%	12·5%
25	33·3
50	100
70	233·3
80	400
85	566·6

All values quoted in the paper are expressed in terms of the air-dry soil.

III.—VARIABILITY OF THE WATER-CONTENT.

So far the water-content has been assumed to be the only measure of the soil-moisture, as in fact it has hitherto been regarded. But it has already been implied that it proves to be a very imperfect index of the soil conditions, not because it varies, for the soil moisture is itself subject to variation, but because it varies irregularly and independently of the humidity of the soil. Broadly, the water-content will by its magnitude suffice to distinguish habitats if the soil is uniform to some depth, but that condition is rarely satisfied in natural habitats and can never be postulated. Still, there is no difficulty in differentiating a heather moor and a cotton-grass moor by the mean water-content of the peat, but in the majority of cases the evidence it affords is inconclusive or contradictory. Even on a heather moor, peat containing only 70 or 80% of water can be shown to be in reality wetter than peat containing 100 or 130% of water.

But the real difficulty in the use of the water-content is met with as soon as the section sampled is not of the same nature at successive depths. Where soils are shallow, as where peat overlies a coarse sand that rapidly passes into rock, or where a woodland humus covers a soil almost free from humus, the active rootlets may occupy both layers indifferently, though, as shown by Woodhead[1] and others, in certain cases these several layers are occupied by distinct members of the association. It was soon discovered that in analyses of such shallow soils the water-content diminished so rapidly at the boundary between the layers that the values were in no wise comparable, in spite of the fact that both related to the same plant. A few illustrations selected from and typical of the earlier stage of this investigation will make the point clear.

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[1] "Ecology of Woodland Plants in the Neighbourhood of Huddersfield." Journ. Linn. Soc. Bot., Vol. XXXVII., p. 333.

Soil No. 13 (September, 1905). *Vaccinium Myrtillus* and *Deschampsia flexuosa* growing in a shallow hollow on a *Calluna* Moor, Yorks.

		Air-dry Peat.		$\frac{\text{Water}}{\text{Humus.}}$
		Water at 15°C.	Humus.	
i.	Loose fibrous peat ½-¾ ins.	176·4%	78·8%	2·23
ii.	Compact peat ¼-¾ ins. ...	61·0	17·4	3·52
iii.	Sandy "sub-peat" 1-2 ins.	21·1	8·1	2·59

Rootlets penetrating ii. and entering iii.

Soil No. 34 (March, 1906). *Vaccinium Myrtillus* and *Deschampsia flexuosa* in Oak Wood (*Q. sessiliflora*), Yorks.

		Air-dry Peat.		$\frac{\text{Water}}{\text{Humus.}}$
		Water at 15°C.	Humus.	
i.	Humus at 1-2½-ins. ...	170·0%	55·5%	3·06
ii.	Sandy soil below i. ...	30·4	10·4	2·92

Rootlets permeating i. and extending into ii.

Soil No. 66 (September, 1906). *Nardus stricta* on *Nardus* pasture, Yorks.

		Air-dry Peat.		$\frac{\text{Water}}{\text{Humus.}}$
		Water at 15°C.	Humus.	
i.	Black soil at ½-1½ ins. ...	67·4%	33·4%	2·01
ii.	Same at 1½-2¼ ins. ...	40·3	18·6	2·16

IV.—WATER-CONTENT A FUNCTION OF THE HUMUS-CONTENT.

In the first two soils it is clear that no significant result can be obtained by averaging such divergent values for the water-content as are revealed by the analyses. The cause for the divergence is not far to seek: it is found in the varying quantity of humus present in the different layers. If then the humus is the disturbing factor, it seems probable that if its influence can be eliminated the successive layers will not prove very different, and the real humidity—the state of wetness—of the habitat can be assessed. This is done by reducing the humus to unity in all cases. In other words the water-content is expressed in terms of the humus-content, and the ratio $\frac{\text{water-content}}{\text{humus-content}}$ which is used as the new index of the soil moisture may be fittingly called the *coefficient of soil humidity*.

The importance of humus in increasing the water capacity of a soil has long been recognized. But the working hypothesis now formulated, is that the humus, as a colloid holds all, or practically all, the water in a humous soil, so that even with relatively small humus-contents the water holding power of the non-colloid constituents may be neglected. Leaving on one side the possibility that in other types of soil colloid clay may have a similar function, it remains to see how far the formula *the water-content is a function of the humus-content* provides in the coefficient of humidity a satisfactory instrument for gauging the soil moisture of a plant habitat.

Turning to the examples given above it is seen that in Nos. 34 and 66 the values of the coefficient in the two layers are practically identical. The natural interpretation of this is (1) that the humus is the sole cause for the difference in water-content; (2) that both layers are equally humid, in the same sense that the atmosphere may be equally humid on two days when the actual "water-content" is widely different. Its absolute magnitude is determined in the one case by the temperature of the air, in the other by the humus of the soil. So the coefficient measures the relative humidity of the soil, whilst the water-content measures its absolute humidity.

In No. 13 the coefficient values are not quite so consistent, but the case is partly chosen for that reason. The uppermost layer, above the roots, in spite of its high water-content has the lowest coefficient, which thereby reveals the superficial drying of the peat during the summer—a fact that could not be demonstrated in any other way. It is also noteworthy that the two habitats represented by Nos. 13 and 34, occupied by the same plants, exhibit very similar edaphic conditions.

Before turning to other examples in confirmation of these conclusions it may be as well to look at another possible explanation of the varying water-content in these soils. It may be argued that we have here merely a variable holard, or total water-content, of no physiological importance and that in spite of this variation the chresard or available water-content may be the same throughout, *viz.*, 20% or thereabouts. This implies a high echard (non-available water-content) in the case of peat, which in itself is not unreasonable, as there are other grounds for considering that bog plants (bog xerophytes) have difficulty in taking up water from wet peat. But this view appears untenable. There is no evidence that as a peat dries out until the wilting point is reached there is any change in the equilibrium between it and the sub-peat as regards the humidity. The evidence all goes to show that drying proceeds *pari passu* in peat and sub-peat. When each has lost all its physiological water, the echard, it is true is considerably higher in the peat than in the sub-peat, but the water is still distributed between the two according to the humus-content of each. The coefficient of humidity is lower than before and has attained its wilting value, but it is still approximately the same for both.

Some wilting experiments on moorland plants[1] carried out in 1910 support this conclusion. On comparing the results obtained in the most extreme soils examined the differences lie within the experimental errors.

Wilting of *Eriophorum angustifolium.*

Air-dry Peat.

	Water remaining (Echard).	Humus.	$\frac{\text{Water.}}{\text{Humus.}}$
Average of four cases	55·2%	71·1%	0·77
,, ,, ,,	43·7	50·7	0·86

Wilting of *Calluna vulgaris.*

Air-dry Soil.

	Water remaining (Echard).	Humus.	$\frac{\text{Water.}}{\text{Humus.}}$
Peat : average of three cases	25·9%	57·1%	0·45
Loam, or sand, ditto	3·0	7·6	0·36

Comparing these with the average coefficients of their natural habitats the inference appears to be that at the wilting-point the coefficients have about one-sixth their normal value. So five-sixths of the total water-content, irrespective of its amount, may be set down as physiological or available water.

V.—THE COEFFICIENT OF SOIL HUMIDITY.

Now that the coefficient of humidity holds out the promise of being a standard index of the soil moisture, it becomes necessary to submit it to as wide a range of tests as possible to ascertain whether its values are sufficiently constant and distinctive to characterise both allied and diverse habitats—plant societies within an association as well as diverse formations.

Seasonal Variation. Many habitats show a sufficiently marked seasonal variation in the soil moisture to be reflected in the coefficient, as is shown in subsequent examples. But unless the seasonal variation is itself the subject of enquiry it seems better to limit the observations to the period of growth, which coincides roughly with the dry (*i.e*,, dry soil) season, between April and September. In no case should samples be taken within a few days of heavy rain and with this proviso, the results are reasonably comparable throughout the season. The ideal time to take samples is towards the end of a two or three weeks' drought, and this can often be done in April, or June, or onwards to September.

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[1] Crump, W. B. "The Wilting of Moorland Plants." Report of the British Association, Portsmouth Meeting, 1911.

Local Soil Variation. Samples to all appearance identical either from the same section, or from adjacent spots always show some, and often considerable variation in water-content. These accidental errors are entirely eliminated by the use of the coefficient of humidity. With this point in view the following samples of woodland soils, each to all appearance uniform, were divided and analysed separately. Their uniformity is confirmed by the results. Frequently when the samples are not as carefully chosen there is a more marked disparity in the water-content.

Ground Societies in Oak Wood on Coal Measures, Yorks., February, 1912.

			Air-dry Soil.		Water.
No.	Society.		Water at 15°	Humus.	Humus.
193.	*Scilla non-scripta*	(α)...	24·4%	6·9%	3·5
		(β)...	30·5	9·3	3·25
194.	*Carex pendula*	(α)...	281·2	30·3	9·3
		(β)...	248·3	26·7	9·28
195.	*Spiræa Ulmaria*	(α)...	92·3	23·1	4·0
		(β)...	90·0	22·0	4·08
197.	*Holcus mollis*	(α)...	31·2	12·9	2·4
		(β)...	28·6	12·1	2·36

The Moor Formation. A brief statement is all that is necessary, as it has been already shown that the various types of moorland on the Pennines are readily distinguished by the water coefficient of the peat.[1] On the *Eriophorum* moor, for example, its value generally ranges between five and seven though it may touch eight when the peat is composed of *Sphagnum.* An even higher value has been found on the lowland mosses of Lonsdale where the dominancy of *Eriophorum vaginatum* is disputed by *Scirpus cæspitosus.* Pools choked with living *Sphagnum* are of frequent occurrence and the peat is at times more than saturated with water so that the coefficient here attains its highest possible value. This has been confirmed experimentally, for when the peat has been saturated with water in the laboratory, its maximum water capacity has been found to be identical with its water-content *in situ.* What an enormous difference can be brought about by even partial drainage of the habitat is illustrated by a comparison of the two analyses below showing (1) the superficial layer possessed by *Calluna* and (2) the undrained moss occupied by *Eriophorum* or *Scirpus*. It is noteworthy that both these habitats may exist side by side, or rather superimposed, the surface roots of the *Calluna* never penetrating the saturated peat a few inches below the surface.

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[1] Crump, W. B. "The Water Content of Acidic Peats." Report of the British Association, Portsmouth Meeting, 1911; *Naturalist*, 1911, pp. 361-2.

No. 166. Moss at Gilpin Bridge, Westmorland, August, 1911.

	Air-dry Peat.		Water.
	Water at 15°C.	Humus.	Humus.
Calluna on surface at 2-5 ins.	112·5%	71·5%	1·57

No. 165. Foulshaw Moss, Westmorland, August, 1911.

	Air-dry Peat.		Water.
	Water at 15°C.	Humus.	Humus.
Eriophorum, &c. at 6-8 ins. ...	865·2%	75·6%	11·4

The *Calluna* Moor is dealt with at length at a later stage. But one example may be quoted here to serve as an illustration of the average conditions, and for comparison with the next analysis.

Calluna vulgaris on *Calluna* Moor, Yorks., August, 1910.

		Air-dry Peat.		Water.
		Water at 15°C.	Humus.	Humus.
106 i.	Compact peat at 1-2 ins.	78·4%	32·2%	2·43
ii.	Ditto at 2-4 ins. ...	81·9	37·0	2·21
107.	Coarse sand at 4-6 ins.	7·7	3·0	2·53

The Heath Formation. Though this may approach the *Calluna* Moor on the one hand, its drier examples stand out in strong contrast as shewn by the following case where *Erica cinerea* was the dominant plant and the light sand had hardly any covering of peat.

Sandy Heath at Bournemouth, August, 1909. *Erica cinerea*, with *Calluna*, *Molinia* and Pines.

		Air-dry Soil.		Water.
		Water at 15°C.	Humus.	Humus.
82.	Sand at 4 ins.	20·2%	25·6%	0·78
83.	Same at 6 ins.	8·0	9·1	0·88
84.	Another at 4-5 ins. ...	11·0	13·8	0·79

Sessile Oak Wood Association. The analyses of Nos. 193-197, already given, show the range of soil moisture met with in an oak wood. Further examples are now quoted to illustrate the seasonal variation of the coefficient.

Complementary Society of *Pteris* and *Scilla* in Oak Woods, Yorks.

	Air-dry Soil.		
	Water at 15°C.	Humus.	$\frac{\text{Water.}}{\text{Humus.}}$
A.—March, 1911.			
128. *Pteris* rhizomes, humous soil at 4-5 ins.	76·8%	19·7%	3·9
129. *Scilla* bulbs, stiff sand, at 8-9 ins.	37·0	8·3	4·47
B.—May, 1911.			
141 i. *Pteris*, humus at 6-8 ins. ...	176·6	64·7	2·7
ii. Ditto, sandy soil at 8 ins.	59·2	20·8	2·8
142. *Scilla*, stiff sand at 10-12 ins.	29·0	7·1	4·1
C.—July-August, 1911.			
153 i. *Pteris*, shale at 3-5 ins. ...	20·0	10·2	1·97
ii. Ditto ditto at 5-6 ins. ...	17·3	9·1	1·90
174. *Scilla*, stiff sand at 6-8 ins.	11·0	5·9	1·87

The problem is here decidedly complex. The bracken, whose rhizomes lie at the junction of two very distinct soils, has a vegetative period extending through the season covered by the analyses. The bluebells, whose bulbs are deeper seated have become dormant and independent of water-supply before the date of the third set. But the selected examples, few as they are, are sufficient to indicate and interpret the habitats. It is true that the seasonal drying is partially reflected in the water-content. But the coefficient demonstrates it much more accurately, showing a drop by August to half its value in the Spring. Further it eliminates entirely the diversity displayed in the layers occupied by the bracken (141 i. and ii.) The zone occupied by the bluebell bulbs has a high coefficient throughout the vegetative season, whereas the bracken has to endure at least a partial drought before the end of the season.[1] All this is in strict accordance with the known preferences of these plants, but the water-content does not suggest that the bluebell habitat is physiologically the wetter one and remains so as long as necessary.

Another pair of comparable habitats, examined on the same day, will suffice to prove the utility of the coefficient of humidity in distinguishing the ground societies within a wood.

[1] With a more extended series of analyses the method developed in Section VII could be applied to these woodland soils and would involve some revision of the values of the coefficient.

Deschampsia flexuosa, dominant on grit boulders and growing in fine sandy humus, Yorks., August, 1911.

	Air-dry Soil. Water.	Humus.	Water. / Humus.
170. At 2-4 ins....	33·3%	44·0%	0·75
172. At 3-4 ins....	24·8	25·3	0·98

Bromus giganteus, in sandy alluvium on edge of a stream, Yorks., August, 1911.

	Air-dry Soil. Water.	Humus.	Water. / Humus.
173 i. Humus in ball of roots...	125·0%	25·4%	4·9
ii. Stiff sand below ...	29·1	5·3	5·4

Though the water-content of 173 ii. lies midway between that of 170 and 172 the coefficient separates the two habitats in the clearest possible way. The woods characterised by stretches of *Deschampsia flexuosa* were first distinguished as "Dry Oak Woods" in the *Flora of Halifax*. The distinction was then based upon the nature of the vegetation, but it is now confirmed by analysis of the soil.

The Calcareous Formation. Through lack of opportunity calcareous soils have not, as yet, received much attention, and it is not safe to draw comparative inferences from a limited number of samples, all taken under the exceptional conditions of the summer of 1911. But the utility of the coefficient of humidity is still apparent.

CALCAREOUS GRASSLAND.

Sesleria cœrulea, in crevices of limestone rocks, North Lancs.

	Air-dry Soil. Water.	Humus.	Water. / Humus.
132. April, 1911	31·4%	37·7%	0·80
135. " "	15·4	17·0	0·90
162. August, 1911	22·3	19·0	1·17

The values of the coefficient are quite consistent in spite of the difficulty of obtaining uniform samples from the pockets filled with limestone chips, whilest the roots penetrate far into the crevices. The slightly higher value in August, in spite of the long drought, is of no importance. It merely indicates a local variation, a crevice more protected from evaporation. But it must be remembered that the Spring is often a season of drought. At the time when 132 and 135 were taken there had been practically no rain for six weeks. So the analyses point rather to uniform conditions and a low humidity in these limestone crevices.

The concluding set is of special interest because it gives the minimum value of the coefficient determined under natural conditions as well as values obtained earlier in the season, though from widely separated localities.

CALCAREOUS WOODLANDS.

Mercurialis perennis in Ash-Oak Wood on Mountain Limestone, North Lancs.

	Air-dry Soil. Water.	Air-dry Soil. Humus.	$\frac{\text{Water.}}{\text{Humus.}}$
133. April, 1911	66·2%	27·1%	2·44
160. August, 1911	13·3	10·2	1·31

Mercurialis perennis wilting in Beech Hangers, on the chalk escarpment, Hants., September, 1911.

		Air-dry Soil. Water.	Air-dry Soil. Humus.	$\frac{\text{Water.}}{\text{Humus.}}$
186	In different woods ...	9·7%	13·6%	0·72
187		12·8	17·6	0·73
188		10·6	10·6	1·00

Much more information must be collected before the conditions of the plant associations on calcareous soils can be compared fully with those of siliceous soils. But from what has been already set out it is clear there is no great disparity in the humidity of the habitats of *Deschampsia* on the grit and of *Mercurialis* on the limestone and chalk. Both appear liable to periods of considerable dryness and of about the same intensity.

The Sand-Dune Formation. The principle that the water-content is a function of the humus-content, that has so far been the sole condition for the determination of the coefficient of humidity, proves to be insufficient in the case of certain soils with a very low humus-content. In the case of sand-dunes, where the humus is less than 1% and the water less than 5%, the ratio water/humus is both high and irregular in value. Obviously this is because the water held by the sand particles is no longer a negligible fraction of the whole water-content. Though allowance might be made for this disturbing factor either experimentally, or by the consideration of a sufficiently large number of analyses, its influence was first detected in another field. As this appears to afford a solution of the problem it appears desirable to use this material for a more critical examination of the coefficient of humidity and this is done from a mathematical standpoint in the succeeding part of this paper.

Heather Moor Association. This habitat is selected for a more searching examination of the soil humidity because whilst the association is very uniform over wide areas the humus-content varies considerably with the depth. The peat is as a rule so shallow that the heather roots regularly pass through it into the underlying coarse sandy soil that may be conveniently called the "sub-peat." The actual water-content of these two layers is not comparable, but physiologically the two seem indistinguishable, so that any satisfactory index of the humidity should have the same value for the two layers and thus be independent either of depth or humus-content.

This heather moor, as developed on the Pennines is a well-known association. The analyses available represent a number of localities in west Yorkshire, and cover the average seasonal range. To make the association more definite, the wetter type of heather moor characterised by the presence of *Erica Tetralix* is excluded from the present enquiry.

The results of the analyses are set out in the following table in order of the humus-content. As elsewhere in the paper the figures i., ii., iii. added to the soil numbers indicate corresponding layers of a section. There is no difficulty in distinguishing a peat from a sub-peat for the table shows that there is a sharp break between the two. It includes only one sample with a humus-content between 10% and 25%, so that whilst a sub-peat contains less than 10 or 15%, a peat never contains less than 25% and rarely less than 30% of humus.

HEATHER MOOR (*Callunetum vulgaris*).

PEATS: at 1 to 3 inches from the surface.

No.	Date.	Moor.	Water Loss at 15° %	% of Air-dry Peat.			Water. / Humus.
				Loss at 100°	Humus.	Mineral Residue.	
			y		x		m
207 i.	April, 1912	Greetland	168·2	12·2	70·8	16·9	2·4
206 i.	,,	,,	135·8	10·7	62·9	26·4	2·16
37	Mar., 1906	Cold Edge	139·4	7·2	49·6	43·2	2·8
99 i.	Aug., 1910	Norland ...	101·4	8·7	48·6	42·6	2·1
63	Aug., 1906	Rumbles...	99·1	7·3	40·0	52·7	2·5
205 i.	April, 1912	Greetland	83·9	7·2	38·4	54·4	2·2
58 i.	June, 1906	Bellhouse	90·8	5·7	37·6	56·7	2·4
106 ii.	Aug., 1910	Erringden	82·0	6·5	37·0	56·5	2·2
11	Sept., 1905	Greetland	73·0	5·6	36·5	57·9	2·0
58 ii.	June, 1906	Bellhouse	71·3	5·0	33·4	61·6	2·1
106 i.	Aug., 1910	Erringden	78·4	6·4	32·2	61·4	2·4
38	Mar., 1906	Cold Edge	84·7	4·8	30·7	64·6	2·76
57	June, 1906	Bellhouse	79·3	5·1	30·0	64·9	2·6
145 i.	June, 1911	,,	45·9	4·7	26·8	68·4	1·7
Mean ...	... ...	... ...	95·2	6·9	41·0	52·0	2·31

Heather Moor (*Callunetum vulgaris*).

Sub-Peats: at 2 to 5 inches from surface.

No.	Date.	Moor.	Water Loss at 15° %	% of Air-dry Peat.			$\frac{\text{Water.}}{\text{Humus.}}$
				Loss at 100°	Humus.	Mineral Residue.	
			y		x		m
102	Aug., 1910	Broadhead	36·6	3·1	14·3	82·5	2·5
58 iii.	June, 1906	Bellhouse	29·4	1·6	9·9	88·5	3·0
206 ii.	April, 1912	Greetland	25·0	2·0	8·3	89·7	3·0
145 ii.	June, 1911	Bellhouse	17·8	1·5	7·1	91·4	2·5
207 ii.	April, 1912	Greetland	20·3	1·3	6·1	92·6	3·3
205 ii.	,,	,,	20·5	1·2	5·9	92·8	3·5
105	Aug., 1910	Erringden	22·2	1·1	5·7	93·1	3·85
99 ii.	,,	Norland ...	16·2	0·9	4·7	94·4	3·2
205 iii.	April, 1912	Greetland	14·0	0·9	4·2	94·9	3·36
107	Aug., 1910	Erringden	7·7	0·7	3·0	96·3	2·5
Mean	... ...	... ...	21·0	1·4	6·9	91·6	3·17

An inspection of the tables shows that the water-content falls steadily with diminution of the humus-content in spite of variation in season and locality. The coefficient of humidity, as expressed by the ratio water/humus, has a mean value of 2·3 in the case of the peats and 3·0 for the sub-peats. There is here a decided difference, which will be considered presently, but within either division there is no great departure from its mean value. The extreme range in either case is about 3 : 2 and this clearly represents the seasonal variation under the conditions already laid down, namely that soils are only sampled after a spell of dry weather. The range could certainly be extended by including more extreme conditions. Analyses made in August, 1911, during the prolonged drought of that summer, yield decidedly lower values for the *Calluna* habitat. But though valuable in determining the minimum value of the coefficient their inclusion here would confuse the general principle.

VI.—Deduction of the Coefficient from the Individual Observations.

Having obtained two series of numbers expressing the conditions of the Heather Moor as displayed in the peat and the sub-peat respectively, the question arises—what is the most suitable treatment of these experimental values to obtain a constant to express the humidity of the *Calluna* habitat? Are the variations from the mean value such as have been already anticipated as inevitable, from the nature of the problem, and in no way invalidating the concept of a constant quantity expressed by the mean? If so what is the best method of deducing the mean value? On the other hand is there any unsuspected cause operating that can be detected and eliminated by mathematical analysis? In particular what is the cause for the higher value of the $\frac{\text{water}}{\text{humus}}$ ratio in the case of the sub-peats?

It is clear, in the first place, that the range of water-content and humus-content is so great even when the sub-peats are separated from the peats that no great importance can be attached to their average values as expressed by the arithmetical means. Still it is noteworthy how closely the means in the case of the peats approximate to the Rumbles Moor sample (No. 63) which is undoubtedly typical of the Yorkshire heather moor.

Attention may therefore be concentrated on the values of the coefficient of humidity expressed by the ratio $\frac{\text{water.}}{\text{humus.}}$

If for a given habitat

$$\frac{\text{water-content}}{\text{humus-content}} = \text{a constant}$$

we have simply a special case of the general equation of the straight line passing through the origin of rectangular co-ordinates x and y viz:—

$$\frac{y}{x} = m$$

$$\text{or } y = mx \quad \dots \quad \dots \quad \dots \quad (1)$$

where m=coefficient of humidity=tangent of the angle the line makes with the axis x.

If the line does not pass through the origin the equation becomes

$$y = b + mx \quad \dots \quad \dots \quad (2)$$

where b is the ordinate at the origin.

The points to be considered are whether the values set out in the last column of the tables conform to a straight line rather than some other curve; and if so, whether it satisfies equation (1) or (2), and then to find the value of m, and of b if required.

When the values of x and y (humus and water) are plotted the the points obtained are so irregularly distributed that it is difficult to decide the slope of the curve by inspection, or even whether it passes through the origin. But no curve other than a straight line corresponds with the points. So a trial may be made with a straight line drawn through the origin and making with the x axis an angle whose tangent is the mean value of the coefficient of humidity so as to satisfy the equation

$$y = mx.$$

Using the values $m=2{\cdot}3$ for the peats, and $m=3{\cdot}0$ for the sub-peats lines are obtained that show the individual points almost equally distributed on either side of the lines. This should be the case and in the case of the peats no further analysis seems necessary and the equation $y=mx$ may be accepted provisionally as a satisfactory solution.

VII.—REDUCTION BY THE METHOD OF LEAST SQUARES.

But in the case of the sub-peats there is an obvious objection to the acceptance of the same equation even when m has a different value. For, in any case, when $x=o$, according to the equation $y=o$, but as a matter of fact, when the humus in the soil is reduced to zero there is still some water held by the soil particles. So that for these soils, with humus-content below 10 or 15% it is necessary to fall back on the equation

$$y = b + mx$$

where b represents the residual water present in the soil independently of any humus.

It is impracticable to find the value of b by the usual method of making $x=o$, and hence $b=y$, because no soil is met with entirely devoid of humus. But the most probable value of both b and m may be calculated from the experimental results by the method of least squares—a method of greater refinement than the occasion requires, but the only one available. If the linear equation is written in the form

$$b + mx - y = o$$

the values of y calculated from the equation will differ from the experimental values y_1, y_2, y_3, corresponding to experimental values x_1, x_2, x_3. Let these differences be δ_1, δ_2, δ_3. Then

$$b + mx_1 - y_1 = \delta_1$$
$$b + mx_2 - y_2 = \delta_2$$

The method of least squares shows that when the sum of the squares of these differences is a minimum the calculated values of the constants b and m are the best that can be deduced from the experimental results, supposing all the observations are of equal accuracy and may therefore be given equal weight.

To obtain the values of b and m in the linear equation

$$y = b + mx$$

the method of least squares furnishes the two equations

$$b = \frac{\Sigma x \cdot \Sigma xy - \Sigma x^2 \cdot \Sigma y}{(\Sigma x)^2 - n\Sigma x^2} \quad \ldots \quad \ldots \quad (3)$$

$$m = \frac{\Sigma x \Sigma y - n\Sigma xy}{(\Sigma x)^2 - n\Sigma x^2} \ldots \quad \ldots \quad \ldots \quad (4)$$

where n=the number of observations.

But if $b=o$ simpler equations may be obtained, for then

$$\frac{\Sigma y}{\Sigma x} = m \quad \ldots \quad \ldots \quad (5)$$

and from equation (3)

$$\Sigma x \cdot \Sigma xy = \Sigma x^2 \Sigma y$$

$$\therefore \frac{\Sigma y}{\Sigma x} = \frac{\Sigma xy}{\Sigma x^2}$$

$$\therefore \frac{\Sigma xy}{\Sigma x^2} = m \quad \ldots \quad \ldots \quad (6)$$

If then the curve passes through the origin there are two alternative methods of calculating the coefficient of humidity (m). Applying these methods to all the values of water-content and humus-content set out in the tables the following results are obtained :—

By Equations 5 and 6

		Coefficient of Humidity (m).	
	n	$\frac{\Sigma y}{\Sigma x}$	$\frac{\Sigma xy}{\Sigma x^2}$
Peats	14 ...	2·32	2·32
Sub-peats	10 ...	3·03	2·91

The two values of m are, in the case of the peats, identical in spite of considerable individual departures from this mean value. So the equation $y=mx$ affords a complete solution and the water-content is found to be a function of the humus-content, and of that alone. This is expressed by the coefficient of humidity.

In the case of the sub-peats the two values are not identical so that the simpler equation is again found to be insufficient. But turning to equations 3 and 4 the following values are obtained by their application to the analyses of the sub-peats :—

	Sub-peats.
Residual water (b)	4·8%
Coefficient of humidity (m) ...	2·33

Hence for the sub-peats

$$y=b + mx$$

and to deduce the value of the coefficient the water held by the soil particles, practically 5% of the air-dry soil, must first be deducted

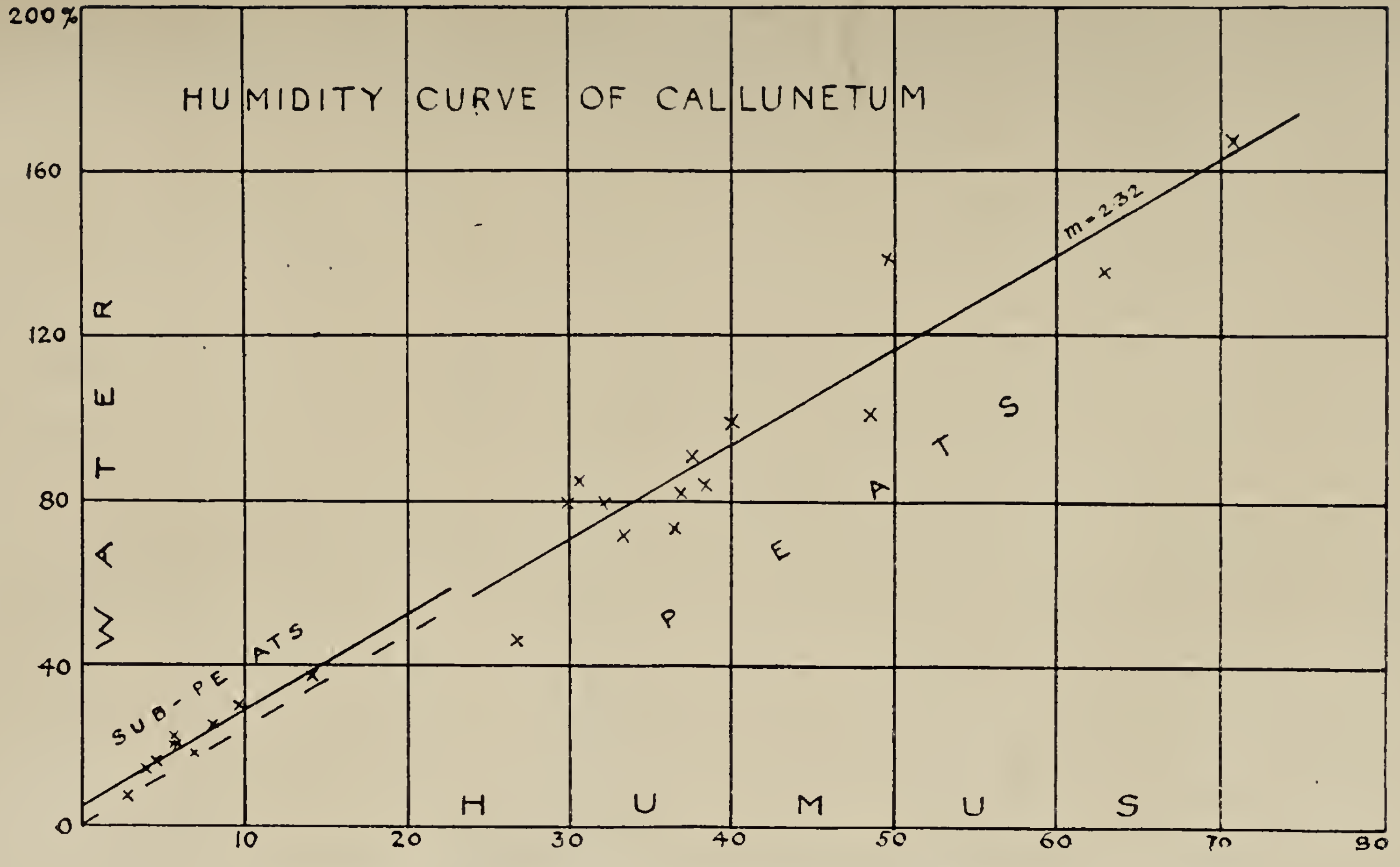

FIG. 1. Humidity Curves drawn from the values deduced by the Method of Least Squares.
(i) Peats — Coefficient of Soil Humidity = 2·32.
(ii) Sub-peats — Coefficient =2·33, Residual Water =5%

and then the remaining water is a function of the humus. Not only is it a function, but it is the same function as in the case of the peats, for the value of the coefficient is the same in each group.

The question naturally arises whether this residual water (b) is itself a constant, or whether it is not a variable depending upon the percentage of earthy (*i.e.*, non-humous) matter in the soil sample. Practically it may be regarded as a constant because it only has to be taken into account when the soils contain upwards of 80 or 85% of earthy matter, so that any variation of the amount is too small to affect the quantity of residual water so long as that is itself as low as the value arrived at above. The nature of the soil particles is likely to have a much greater influence on its magnitude. The sub-peats examined are all coarse sands composed largely of quartz-grains and free, or nearly so, from clay. In this case the residual water does not exceed 5% of the air-dry soil. What it may amount to in the case of clay soils is still unknown.

Accepting 5% as a sufficiently accurate allowance, in each case it is now possible to deduct this from the total water-content of the sub-peats tabulated above and so obtain the true coefficient of humidity for each sample. The improvement affected by this deduction is apparent on comparing the values of the coefficient in the samples that include both peats and sub-peats.

Coefficient of Soil-Humidity in successive layers after deduction of Residual Water (5%).

Soil No.		m	Soil No.		m
58 i.		2·4	205 i.		2·2
ii.		2·1	ii.	(3·5)	2·6
iii.	(3·0)	2·4	iii.	(3·4)	2·1
99 i.		2·1	206 i.		2·16
ii.	(3·2)	2·4	ii.	(3·0)	2·4
145 i.		1·7	207 i.		2·4
ii.	(2·5)	1·8	ii.	(3·3)	2·5

The uncorrected values of m for the sub-peats are placed within brackets.

Before finishing with the humidity equations it is perhaps worth while to enquire what values would be obtained in the case of the peats if the equation $y=b+mx$ applied to them. Using equations 3 and 4 the method of least squares gives the following results:—

	Peats.
Residual Water (b)	—1·5%
Coefficient of Humidity (m)	2·35

The value of *m* is nearly the same as that already established, but *b* instead of being *nil* has a small negative value. No physical meaning can be attached to the negative sign, and its appearance only illustrates the extreme delicacy of the method of least squares. The curve obtained by it is sensitive not only to deviations from the mean but to their positions in the set of observations. Here it is undoubtedly peat No. 145 i. that having a value below the average, depresses the curve slightly below the origin because of its position at the end of the list. For the purpose in view and with the data available in soil analyses the method of least squares is almost too refined an instrument. With only half-a-dozen analyses the numbers obtained by its use may be quite misleading. Though further investigation may lead to a revision of the values set out in this paper, the material employed seems sufficient to furnish a fairly close approximation to the true magnitude of the coefficient of soil-humidity in the case of the Heather Moor Association, and to establish the principles involved in its determination.

VIII.—THE INFLUENCE OF CLAY ON THE SOIL MOISTURE.

If the method already applied to non-humous soils to determine the water held by the soil apart from the humus is sound, it follows that if a soil contains clay this will partially control the water-content even when present in much smaller quantity. Though such an effect has been anticipated no data are yet available for determining the coefficient of soil-humidity in clay soils. Nor is it clear whether the coefficient could be taken as the ratio $\frac{\text{water-content}}{\text{humus} + \text{clay}}$ as the joint effect of the two colloids may not be equal to the sum of their individual water-holding power. There is also the difficulty that in clay soils the loss on ignition includes more than the humus.

But an important paper on "The Moisture Equivalents of Soils"[1] by L. J. Briggs and J. W. McLane, that has only come to the knowledge of the author after the completion of this paper throws considerable light on the subject. Briggs and McLane's "moisture equivalent" is the percentage of moisture a soil can retain when subjected to a centrifugal force about 3,000 times the force of gravity. The authors show that the magnitude of this moisture equivalent for any soil depends almost wholly and equally upon the clay and the humus present. The silt exerts an appreciable though smaller effect, but all the coarser particles show practically no retentive action.

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[1] U.S. Department of Agriculture, Bureau of Soils, Bulletin No. 45, Washington, 1907.

Put as an equation their result is

$$M = 0{\cdot}13\ C + 0{\cdot}62\ (D + E),$$

where M is the Moisture Equivalent

C=per cent of silt (0·05—0·005 *mm.*)

D=per cent of clay (0·005—0· *mm.*)

E=per cent of organic matter determined by the chromic acid combustion method.

Neither M nor E is identical with the constants adopted in this paper, but there is a general correspondence. So it seems likely that the water-content of a soil depends primarily, and approximately to an equal extent upon the clay and humus-contents. In the case of a clay soil then it may be anticipated that the equation

$$y = mx + nz$$

will hold good; or if n proves to have the same value as m

$$y = m\ (x + z)$$

where z is the percentage of clay.

Though the method of investigation and the types of soil are totally different in the two cases, the conclusions arrived at in the present paper receive independent confirmation in the results of Briggs and McLane's study of agricultural soils. Both deduce a linear equation to express the equilibrium under stated conditions; both point to the soil-moisture under such conditions being an adequate and simple index of the soil.

IX.—Ecological Considerations.

In conclusion it seems desirable to glance at the broader aspect of the problems involved in the present investigation of the soil moisture in relation to the plant association. If the coefficient of soil humidity is to be of service in ecology it will only be by a thorough study of definite habitats, and the lines on which this can be prosecuted to advantage may be indicated as follows:—

(1). The mean value of the coefficient of soil-humidity m is the most important constant to be ascertained for every association whose distribution and existence are determined by soil moisture. This mean value, obtained by methods already described, may be indicated by M.

(2). But the coefficient for every such association will prove to have a considerable variation from its mean value. Given a sufficient number of estimations this variability would be best expressed by the "standard deviation," but in actual practice it would be sufficient to ascertain the maximal and minimal values, say m_1 and m_2, of a considerable number of estimations. These values m_1 and m_2 mark the limits of the association and are probably determined by competition with other associations whose M values are different.

(3.) There will also be a supra-maximal (m'_1) and a sub-minimal (m'_2) value of m for any association or its component members, determined not by competition, but by the physiological relations of the root-systems with the soil-water. When these values are reached and maintained the association can no longer continue to exist.

Opportunities for determining these supra-maximal and sub-minimal values may not be frequent, and usually they may not be distinguishable from the maximal and minimal values. But there are occasions when they cannot be ignored. The case already quoted where *Mercurialis* was wilting in September, 1911 is one in point, where the sub-minimum had been reached, for though the plants recovered it was only because the existing state was not maintained, and clearly there was no competitive factor. Again the gradual accumulation of peat may of itself raise the coefficient to such a supra-maximal value that the existing association can no longer maintain its position, just as artificial drainage may lead to the extinction of the association by reducing the coefficient to its sub-minimal value.

(4). The sub-minimal value of the coefficient for any association will represent, and be the appropriate expression of the echard.

(5). The soil moisture index of an association will be fully determined by finding the values of m_1, m_2, m'_1, m'_2 and M.

These considerations only hold good at present in cases such as have been considered, where the humus practically holds all the soil water, *i.e.*, where there is no "free" water in the substratum, nor sufficient colloid clay to affect the balance.

It only remains for me to express my thanks to Mr. A. G. Tansley for helpful criticism of the paper, for calling my attention to the work of Briggs and McLane and for the suggestions utilized in the closing paragraphs.

THE HEATH ASSOCIATION ON HINDHEAD COMMON.

BY

F. E. FRITSCH, D.SC., PH.D.,

Professor of Botany, East London College (University of London),

AND

WINIFRED M. PARKER, B.SC.,

Demonstrator in Botany, East London College (University of London).

[WITH PLATE V AND FOUR FIGURES IN THE TEXT].

THE following paragraphs give a brief account of an investigation into the heath vegetation on Hindhead Common, which is being carried out by the staff and students of the Botanical Department of the East London College. Although the investigation is at present only in a preliminary stage, it is hoped that a short account of what has been done may be of interest. The area concerned lies to the right of the road leading from Hindhead to Guildford (*i.e.*, on the side opposite to that on which the famous "Punch Bowl" is situated); it is well suited for the purposes of such an investigation, as it is traversed only by a few paths and is very little frequented. The area has been visited annually in July and, in the present year, also in January and April. Our aim for the present has been chiefly to map a representative portion of the vegetation and to commence studies on the re-colonisation of new ground.

The area is situated on the Hythe beds of the Lower Greensand. Soil borings show that beneath a surface layer of peat varying from 1½ to 3 in. in thickness there ordinarily lies a layer of dark (rather peaty) sand (4 to 5 in.) and then a stratum of fine light-coloured sand (5 to 6 in.); at some points this lower stratum is rather stony. There are indications that the character of the soil (especially as regards its degree of coarseness) varies somewhat on different parts of the heath, but our investigations on this point are at present insufficient. Over a very considerable portion of the area an inch or so of the surface of the soil is charred, hard and brittle; it is astonishing how long the soil appears to retain this mark of a former fire, which must in some cases be at least ten years old.

In preparing the map (Text-fig. 1) the method adopted has been that of laying out the ground into 100 feet squares[1] and mapping each separately. The part of the area dealt with in the present account (cf. the map and the two sections, Text-figs. 1 and 2) comprises about half the Hindhead Common proper. It consists of a flat-topped central ridge, skirted by two valleys (A and B), each of which is traversed by a narrow (little used) pathway; the broad central ridge is totally undisturbed except for a clearing about 12 ft. wide extending along its whole length.[2] The two valleys exhibit a gradual downward slope towards the south-west and are bounded on one side by the steep inclines of the central ridge and on the other side by equally steep slopes—as shown in the sections (Text-fig. 2), in which, however, the vertical scale is exaggerated. The central ridge has a broad, almost flat top, the width of which gradually diminishes in the south-westerly direction (cf. especially the sections), where the ridge ultimately slopes down rapidly to the path connecting valleys A and B. The north-easterly part of this ridge is a broad flat plateau and does not begin to slope appreciably in the south-westerly direction until a point about 1,000 ft. from the top of the area shown in the map is reached; after that the slope towards the south-west is very gradual for a time, until near the end of the ridge a steep incline leads down to the path connecting valleys A and B at the extreme south-west end of the area.

A.—CONSTITUTION OF THE HEATH-VEGETATION.

The valleys are partly occupied by a dense growth of tall *Ulex europæus* with very extensive tracts of high-growing bracken (*Pteridium aquilinum*); intermingled are a number of other woody species (especially *Rhamnus Frangula* and *Ulex minor*), together with a considerable number of herbaceous forms (cf. below, p. 156). The distribution of *Ulex europæus* on the area concerned quite agrees with other observations on the occurrence of this species on heaths.[3] It is practically confined to the neighbourhood of the pathways, from which however at some points it extends for some distance upwards on to the slopes of the valleys. A very few isolated patches are found on the top of the ridge, their presence there being at present difficult to explain; but these patches are really quite insignificant as compared with the extent of the remaining vegetation.

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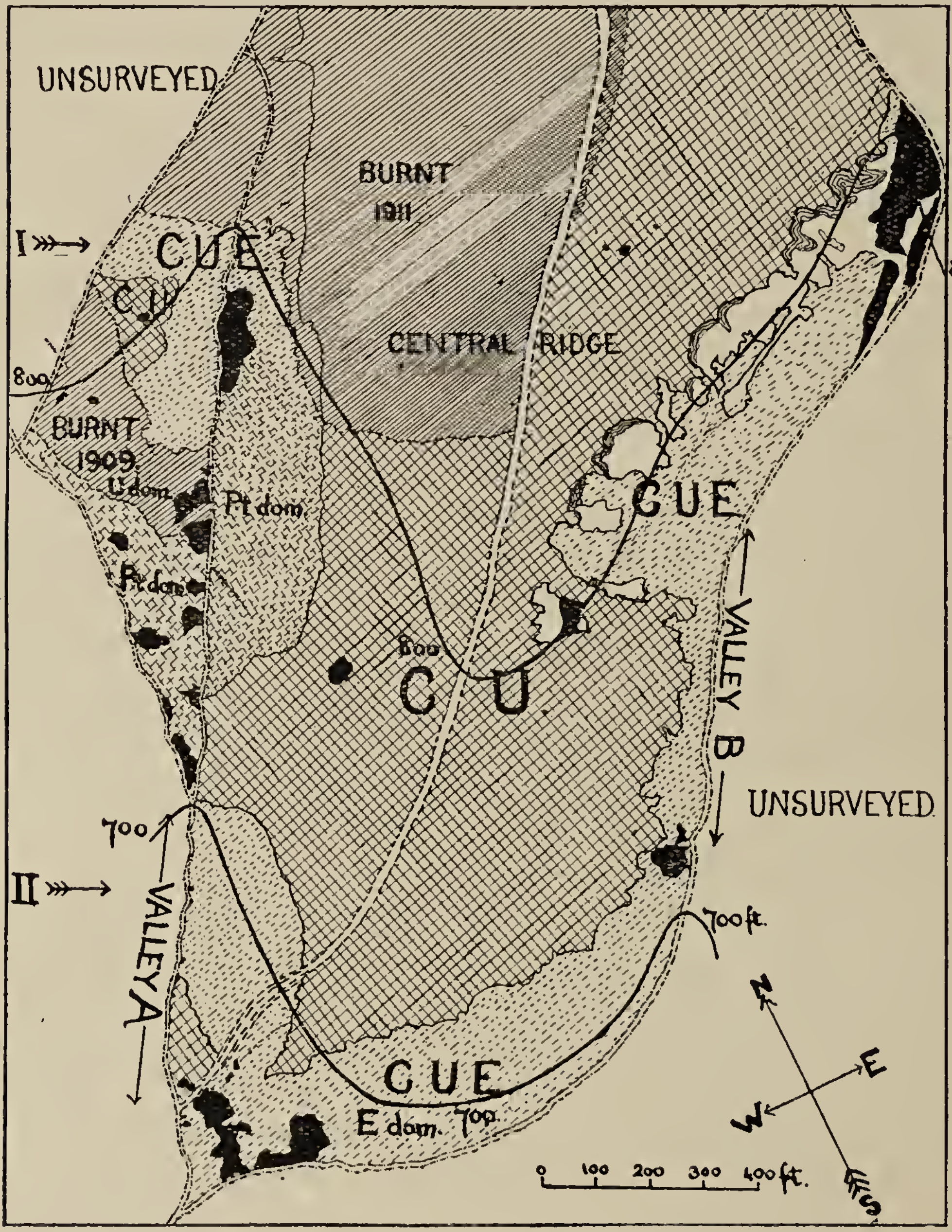
[1] Oliver, F. W., and Tansley, A. G. "Methods of surveying vegetation on a large scale." NEW PHYTOLOGIST, Vol. III, 1904.

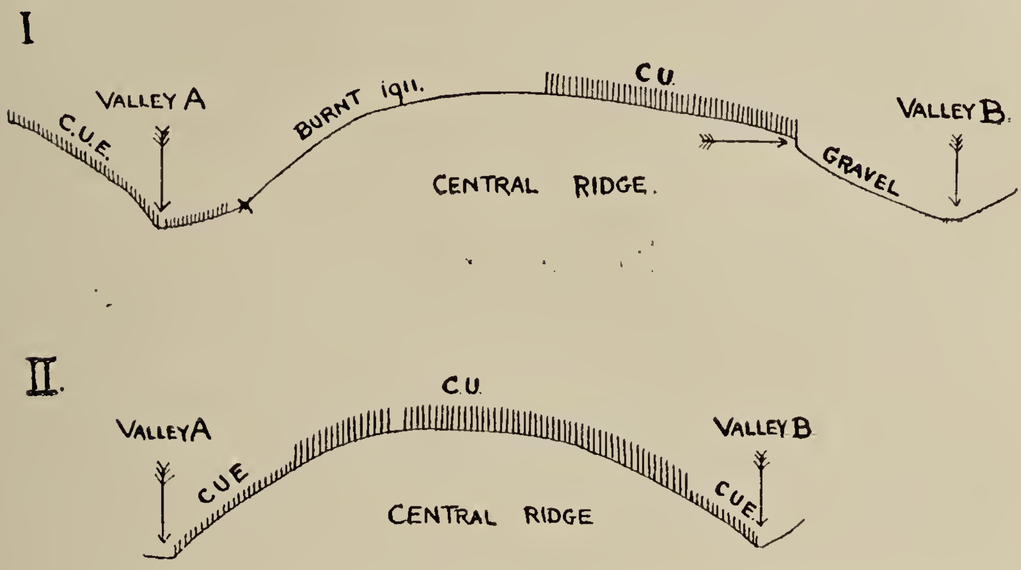
[2] A second smaller clearing (not shown in the map) was made in the autumn of 1911.

[3] Tansley, "Types of British Vegetation," 1911, pp. 105-106. *Cytisus scoparius* shows a similar, but more limited distribution, being found only in the lower part of valley A on either side of the pathway.



Text-fig. 1. Map of part of Hindhead Common at present surveyed. Pathways indicated thus =:=:=, clearings indicated thus = = =. The contours are indicated by heavy lines, and have been transferred from the Ordnance Survey maps. Areas of the common recently burnt are closely shaded. The black patches mark the positions of more or less extensive groups of *Ulex europæus*. The unshaded areas on the eastern slope of the central ridge represent exposed tracts of gravel (cf. Text-fig. 2). C U, *Calluna-Ulex* facies (cf. p. 153); C U E, *Calluna-Ulex-Erica* facies (cf. p. 154): Pt., *Pteridium aquilinum*. The thin irregular line running almost vertically through the area burnt in 1911 marks the former limit of the C U and C U E facies in this region.

The distribution of *Ulex minor* Roth (= *U. nanus* Forster) is very different from that of *U. europæus*. Together with *Calluna*, it is the dominant feature of the vegetation over the greater part of the heath. Two (if not three) forms of this species must be distinguished. In the valleys, along with *U. europæus*, there grows



Text-fig. 2. Diagrammatic sections of the part of Hindhead Common at present surveyed. The points at which the sections are taken are indicated by arrows at the left-hand side of the map on the opposite page. The cross to the right of Valley A shows the position of the former limit of C U and C U E facies before the fire of 1911. The horizontal scale is the same as that of the map; the vertical scale is exaggerated. The horizontal arrow in section I. indicates the point at which the land-slide (p. 161) has taken place.

an upright form, differing markedly in habit from that usually described in floras. This upright form has generally no procumbent branches whatever, but an uprising main stem, varying in height from 2¼ feet to 4 feet.[1] The lower part of the main stem is mostly unbranched, while near the top numerous branches arise. Among the growth of low *Calluna* on the slopes of the valleys another form is found. In this case branching generally takes place freely from the base of the plant, the branches being for the most part procumbent. Occasional specimens, however, show one or more upright (or obliquely ascending) shoots, which grow to a height of 1½-2½ feet; these upright shoots (generally bare below and well branched above) are quite similar in habit to the upright form found in the valleys, and are the only part of the plant that appears above the level of the surrounding heath-vegetation.

As already indicated it is only occasional specimens of *Ulex minor* on the valley-slopes that show the upright shoots just described; a large number of specimens are entirely procumbent and of the type usually described in floras. In the zone of tall *Calluna*, found on the top of the central ridge, (cf. below, p. 152) the completely procumbent type is decidedly more prevalent than on the valley-slopes, although even on the top of the ridge occasional specimens with upright branches occur, these branches however never arising above the *Calluna*-level. It must be realised therefore that over the greater part of the Hindhead heath the *Ulex minor* is hidden from view by the growth of other constituents of the vegetation and is only visible at close range. At many points the branches of the procumbent form give rise to compact cushions, almost completely hiding the underlying soil by their dense branching. Such cushions are beautifully seen on areas recently burnt (Pl. V, fig. 4) and on the exposed gravel slopes on the north-eastern side of the central ridge (cf. below, p. 162).

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[1] The tallest specimen measured was 4 feet 2 inches high.

The following forms of *Ulex minor*[1] can thus be distinguished on the Hindhead heath:—(a) the normal procumbent form, prevalent among the tall *Calluna* found on the top of the central ridge and at some other points, and very common on the valley-slopes; (b) an upright form, generally without procumbent branches, and found only in the valleys; (c) an intermediate form, showing both procumbent and upright branches, frequently found on the valley-slopes and more rarely on the top of the central ridge.

There appears to be a marked tendency towards the production of upright shoots in *Ulex minor*, but it does not seem except in the valleys and on the lower parts of the valley-slopes that they can long withstand the conditions to which they are subjected. The most acute of these will be the drying influence of the prevailing winds. Many of the upright branches, especially on the upper parts of the slopes, show more or less advanced stages of drying up, and it would seem as though in these positions only those upright branches ultimately survive as are well protected from the prevailing winds by dense growth of the surrounding heath-plants. Many of the "intermediate forms" (*c* above) will thus by dying away of their upright shoots ultimately come to be of the normal procumbent type. When the present investigations have been carried on a few years longer the problem of the different growth-forms of *Ulex minor* will be definitely solved.[2]

We may next proceed to consider the constitution of the heath-association on the area concerned. The top and the upper slopes of the ridge are occupied by a growth of very tall *Calluna* ($2\frac{1}{2}$-$3\frac{1}{4}$ feet high and 10-14 years old). Standing on the flat top of the ridge one sees a monotonous expanse of ling, interrupted by an

[1] On some of the other heaths in this part of Surrey the upright form of *Ulex minor* is much rarer.

[2] About fifty marked plants of *Ulex minor* are under observation.

occasional specimen of *Pinus* or *Betula* or one of the isolated patches of *Ulex europæus* above referred to. This vegetation is however not nearly as pure as it appears at first sight, for not only is the ground very largely occupied by the procumbent form of *Ulex minor*, but scattered plants of *Erica cinerea*, *E. Tetralix* and *Vaccinium Myrtillus* are to be found over the whole surface. Except for the *Calluna* and *Ulex minor* however no other form can be regarded as dominant (C U facies, cf. map). The growth of the ling on this part of the heath is very dense, for the plants, although their bases are quite widely separated from one another, branch very profusely above, so that the upper branches of adjacent plants are generally close together. A striking feature is the very uniform level of the top of this *Calluna*-zone. This appears to be due to the fact that projecting tips, which grow beyond the level of the surrounding growth, tend to dry up and die away—a fact, which may be in part responsible for the very profuse branching exhibited by the plant in its upper portion. It is probable that the vertical growth of this tall *Calluna* takes place very slowly, although we have no satisfactory data as yet on this point.

Except where *Ulex minor* covers the ground there is thus plenty of room for the growth of other plants, but this growth has to take place under the shade of the *Calluna*, and the conditions are evidently not favourable.[1] *Erica* and *Vaccinium* are chiefly found where there is a break in the general continuity of the *Calluna*-level, whilst where the latter grows densely, the ground often bears no growth except for Mosses (*Polytrichum juniperinum*, more rarely *Leucobryum*) or Lichens (chiefly species of *Cladonia*). Bracken is altogether wanting over considerable areas of the ridge-top, and, when present, is represented only by isolated plants or small patches, the fronds of which rise to only about half the height of those in the valley. It is probable that the ridge-vegetation illustrates the oldest phase of the heath on the area under discussion (cf. below, p. 161).

This *Calluna-Ulex* vegetation extends downwards for a varying distance on to the slopes of the central ridge, but is terminated by a sharp limit (no doubt representing the line of termination of a heath-fire), visible even from afar (cf. Pl. V, fig. 1). In the lower half of the area concerned the C U facies extends down at some points to near the bottom of the valleys, actually reaching the path in valley A for a stretch of about 200 feet. A small distinct patch of the C U facies is also found along the path in valley A at the point where the clearing from the central ridge reaches this path (cf. the map).

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[1] cf. Tansley, loc. cit., p. 104.

Below the limit of the *Calluna-Ulex* vegetation the north-western, south-western and south-eastern slopes of the ridge bear a dense vegetation in which *Calluna*, *Ulex minor*, *Erica cinerea* and, to a lesser extent, *Vaccinium Myrtillus* compete for dominance (C U E facies). The *Calluna* in this region rarely exceeds a foot in height and is about five years old. *Ulex minor*, though largely procumbent (cf. above, p. 151), shows rather frequent uprising branches, such specimens alone appearing above the level of the surrounding *Erica* and *Calluna*. Bracken is much commoner (and provided with rather taller fronds) over the whole of this area than on the ridge-top, and for a stretch of about 600 feet in the middle of the north-western slope becomes a dominant, the green sheet formed by its fronds in summer being a very conspicuous feature. Specimens of *Pinus sylvestris*, *Rhamnus Frangula*, *Betula alba*, *Pyrus Aucuparia*, *Pyrus Aria* and *Ilex Aquifolium* are scattered in this low *Calluna*-zone, being generally more abundant on the lower parts of the slopes, especially near the lower end of valley A. Their presence however in no way affects the general character of the heath-vegetation among which they occur. The abundance of young plants of some of these species (especially *Betula*, *Pinus* and *Rhamnus*) at some points indicates a trend in the direction of a birch-heath. On the south-western slopes *Erica cinerea* becomes a dominant,[1] the heath at this point in July appearing as one purple stretch, when seen from a distance.

On the opposite (south-east) slope leading down to the valley A we have a repetition of the vegetation on the north-west slope. Most of this region is occupied by the C U E facies with dominance of *Pteridium* for a stretch roughly corresponding with that on the north-west slope. Only a small patch of the C U facies is found near the path on the extreme left of the map.

A number of grasses occur on the heath (*Deschampsia flexuosa*, *Molinia cœrulea*, *Triodia decumbens*, *Agrostis canina*), but of these only the first two play a really important part. *Deschampsia* is on the whole most abundant on the top of the ridge and on the upper part of the slopes, while *Molinia* is found more especially in the valleys and along the sides of the slopes. Analyses have shown that the water-content of the soil is appreciably less on the top of the ridge than on the sides of the slopes and in the valleys, and it is possible that this factor determines the distribution of the two important grasses, although we should not like to accept such a conclusion without further evidence. It will be well at this point to refer to the distribution of another member of the heath-vegetation. In the heaths of other parts of England *Erica Tetralix* appears to favour the damper places. We can find no evidence of this on the heath at Hindhead, for this species shows no special restriction to certain points, and is, if anything, most abundant on the relatively dry summit of the ridge.[1]

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[1] This dominance of *Erica cinerea* on southerly and south-westerly slopes is a general feature in this part of Surrey. Standing on Gibbet Hill in July nearly all the southern slopes visible from there appear a deep purple.

There is no difference in specific constitution between the different facies of the *Callunetum* on the Hindhead heath, but, as the above description will have shown, the relative grouping of the species varies. The following is a complete list of the members of the *Callunetum*, found on the area at present mapped:—

Calluna vulgaris
Erica cinerea
,, *Tetralix*
Vaccinium Myrtillus
Ulex europæus (only isolated patches)
,, *minor*
Potentilla erecta (isolated)
Cuscuta Epithymum (rare, cf. p. 159)
Agrostis canina (rare)
Deschampsia flexuosa
Molinia cærulea
Triodia decumbens (rare)
Rhamnus Frangula
Betula alba
Cratægus monogyna (rare)
Pyrus Aucuparia
,, *Aria*
Ilex Aquifolium
Pinus sylvestris
Pteridium aquilinum
Blechnum Spicant (rare)

Along the edges of and in the immediate neighbourhood of the pathways a much larger number of species are found. Some of these are "weeds" but many are characteristic of southern *Calluna*-heaths[2] or of grass-heaths[3], but on the Hindhead Common are either strictly confined to the paths or only penetrate into the heath proper for a distance of 20–30 feet at the utmost from the paths. The following is a list of these species:—

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[1] On the part of Frensham Common lying in the neighbourhood of the Little Pond, however, *Erica Tetralix* shows a decided preference for the damper ground. The heath on this part of the common consists of practically nothing but low *Calluna* (about 1 foot high) with an almost complete covering of *Cladonia* on the soil. In the neighbourhood of the water, however, *Erica Tetralix* appears in abundance, at some points even extending right into the marsh bounding the pond.

[2] cf. Tansley, Types, p. 105.

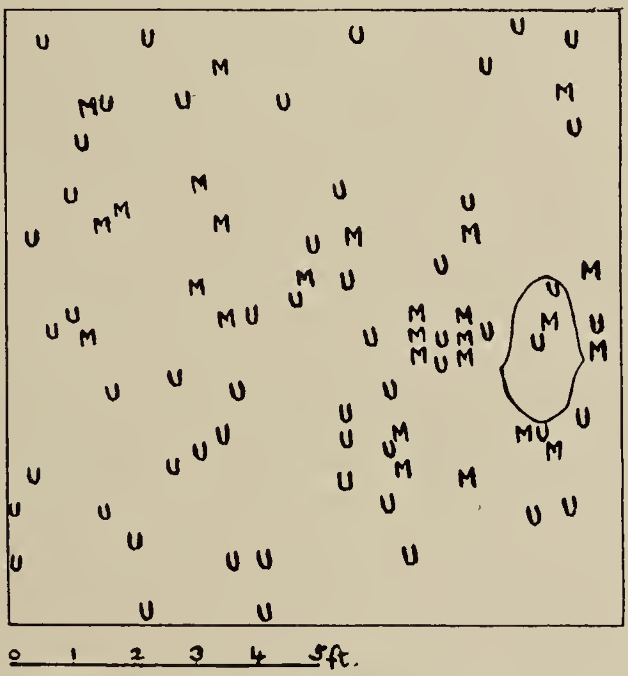
[3] Tansley, pp. 95, 96.

Anemone nemorosa
Viola tricolor
Cerastium viscosum
Stellaria graminea
Spergularia arvensis
Hypericum pulchrum
Ulex europæus (cf. p. 149)
„ *minor* (upright form, cf. p. 151)
Cytisus scoparius (cf. p. 149, footnote)
Trifolium pratense
Rubus spp. (incl. *R. Idæus*)
Potentilla erecta
Galium saxatile
Achillea Millefolium
Hieracium boreale (agg.)
Hypochæris radicata
Erigeron canadense
Centaurea nigra
Chrysanthemum Leucanthemum
Solidago Virgaurea
Campanula rotundifolia
Veronica officinalis
Digitalis purpurea
Teucrium Scorodonia
Plantago lanceolata
„ *major*
Rumex Acetosella
„ *crispus*
„ *obtusifolius*
Carex sp.
Anthoxanthum odoratum
Agrostis alba
„ *vulgaris*
Festuca ovina
„ *rubra*
Holcus lanatus
„ *mollis*
Bromus madritensis
„ *mollis*
Lolium perenne
Cynosurus cristata
Dactylis glomerata
Juncus effusus

Apart from these, all the members of the *Callunetum* (except *Pinus* and *Blechnum Spicant*) occur more or less abundantly in the immediate neighbourhood of the pathways. Near the upper end of valley A (but below the burnt zone) the *Callunetum* is extending across the narrow pathway to the elimination of the other forms previously found there.

B.—Recolonisation on the Hindhead Heath.

A considerable number of observations have been made on the recolonisation of burnt portions of the heath. A small area of the common situated on the south-eastern slope of valley A had been burnt some little time (1909) before we commenced work and a much larger portion (the greater part of which had already been mapped) was burnt in August, 1911. The latter may be considered first. Vegetation soon reappears on such burnt areas. As early as January (1912) *Ulex minor* (also *U. europæus* in the valley) was found sprouting afresh, while numerous seedlings of *Ulex* were growing on the ground. A considerable area of the burnt ground bore a growth of *Pyronema confluens*, but apart from this and the *Ulex* there was no other vegetation. In April of this year the fungus had disappeared, but otherwise the vegetation of the burnt patch showed little change. On some parts of the burnt area nearly every plant of *Ulex minor* was sprouting from the base, the new growth being very closely adpressed to the surface of the ground as a general rule (cf. p. 152 and Pl. V, fig. 4); at other points the *Ulex*-plants over an area of two or three square yards showed no sign of resuming growth. Numerous *Ulex*-seedlings were present, but their number in comparison with January seemed to have diminished, and from other observations it appears very probable that only very few of them prosper. At some points on the burnt patch *Molinia* was reappearing, this growth again arising from the old plants (Text-fig. 3). Here and there very isolated fronds of *Pteridium* were coming up, but no other forms yet showed any indication of growth. By July of this year a vigorous growth of the sprouting gorse had taken place, sufficient to give a greenish tinge to the whole area when viewed from a little distance. The seedlings of *Ulex minor* were however doing rather badly and gave no great promise of future success. This is in marked contrast to the behaviour of the seedlings of *U. europæus* on the part of the burnt area situated in the valley A; many of these looked very robust and had attained a height of 6-8 ins. above the level of the ground, their growth being no doubt favoured owing to the protection afforded to them by the dense mass of tall bracken that occupies the valley (cf. above). A considerable number of *Vaccinium*-shoots were now



Text-fig. 3. Chart to show recolonisation on burnt heath; April, 1912. Every plant is indicated. M, *Molinia*; U, *Ulex*.

arising from the old plants on the burnt area, and an occasional sprouting *Calluna* and *Erica* were also observed, while seedlings of the two last-named forms, and especially of *Erica* were rather numerous at some points.[1] Most of the old *Calluna* and *Erica*-plants however still showed no signs of life.

It may be added that although the area of ground burnt in 1911 included parts of both low and tall *Calluna*-zones (the former limit of which is shown on the map by a thin line), there was no outward difference in the method of colonisation over the whole region.

These observations tend to indicate that the typical heath-representatives are mainly stationary and reappear again in exactly the same positions as they occupied before a fire. A study of the small zone burnt before the survey was commenced leads to the same conclusions. This zone was first examined in July, 1910. At this time there were still appreciable pieces of bare, charred ground between the closely adpressed growth of the numerous *Ulex minor* plants which were sprouting from below. There was also a considerable growth of bracken, due to this burnt area lying within the zone in which *Pteridium* is a dominant (cf. above, p. 154). A few specimens of *Calluna* were found sprouting from the base of the old plants, and there were a considerable number of *Ulex* and some *Erica* and *Calluna* seedlings. A later examination (undertaken in April, 1912) showed that the ground had progressed further in the direction of the typical heath-vegetation. A good deal of sprouting *Erica cinerea* and *Vaccinium Myrtillus* was now present, so that by this time (probably about three years after the fire) all the typical representatives of the flora had reappeared, although the *Ulex* was still by far the most important form. While much of the *Erica* and *Calluna* had arisen from the old plants, there were quite a considerable number of young plants that had developed from seedlings—in fact in the case of *Calluna* it seems that its reappearance may be largely due to the development of seedlings and only to a smaller extent to sprouting from the old plants. In the case of the *Ulex minor*, however, a prolonged search is necessary to find a plant that has grown from seed,[1] and it is quite certain that the bulk of the numerous seedlings of this form, that first appear on such burnt ground, are unsuccessful.

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[1] It is interesting to compare the recolonisation of a part of the "Punch Bowl" that was also burnt in August, 1911. The vegetation on the burnt slope before the fire consisted of a dense growth with *Calluna*, *Pteridium* and *Vaccinium* as dominants, the two species of *Erica* as well as *Ulex minor* being quite scantily represented. In June of this year this area showed a great profusion of bracken, more strikingly developed than on the unburnt part close at hand. The next most important forms were constituted by the sprouting *Vaccinium* and by grasses. The scanty *Ulex*-plants were for the most part sprouting, but owing to their small numbers failed to give any stamp to the vegetation. The rather abundant *Calluna*-plants showed no signs of life.

The young growth on the burnt patch just described has been much infested with *Cuscuta Epithymum*[2] (cf. Pl. V, fig. 5, observed on *Erica cinerea*, *Calluna*, *Vaccinium*, *Ulex minor*). This parasite does not appear to make much headway subsequently, as it is almost absent from the greater part of the heath, although commonly found in the clearing on the top of the central ridge, where there is likewise abundant young growth of the heath-plants. It is noteworthy that on such young ground as is furnished by the burnt patches under consideration a number of species appear in small numbers, which are not found on other parts of the Hindhead heath. Some of these are characteristic representatives of other heath-floras (e.g., *Potentilla erecta*, *Teucrium Scorodonia*, *Carex pilulifera*).

The observations above detailed make it probable that the bulk of the plants appearing on such burnt ground owe their existence to the sprouting of new growth from the bases of the old plants, whose subaërial parts were destroyed by the fire. In this connection it is noteworthy that the species composing the *Callunetum* on the Hindhead heath (see the list on p. 155) are only those which can survive being burned over and over again, and this may account for the comparative paucity of the flora. It is probable that a number of plants are completely killed by the heat[3], and this may apply particularly to the relatively shallow-rooting *Calluna* and *Erica*, but even in these two cases a considerable number of plants certainly regenerate by sprouting. We thus obtain the conception of a possible repeated recovery from consecutive heath-fires, after each of which the vegetation passes through the preliminary phases indicated above, until it arrives at the stage of the fully developed heath. We have no doubt that the low *Calluna*-zone (C U E facies, cf. p. 154) marks a further phase in recuperation, in which the *Calluna* with a number of competitors is slowly attaining to complete dominance. We think that the final stage (as far at least as it is exhibited on the present area) is exemplified by the tall *Calluna*-zone occuring on the top and upper slopes of the ridge and at one or two other points (C U facies, cf. p. 153).[4]

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[1] The main axis of these seedlings exhibits little growth and numerous prostrate laterals soon arise from its base, so that the procumbent habit is assumed at a very early stage.

[2] This also appeared this July on the *Ulex minor* on the ground burnt in 1911.

[3] *Ulex minor* sometimes fails to sprout over areas of several square feet.

[4] cf. Warming "Oecology of Plants" (1909), pp. 354-355.

This last point requires some further consideration. In view of the fact that the C U facies is largely confined to the top and upper parts of the central ridge, it might be supposed that the C U and C U E owed their distinction to the slightly different habitats or to soil-conditions. These possibilities have not been disregarded, but there are, we think, important objections to such a view, which may be briefly summarised as follows:—

(i) The C U facies is not entirely confined to the top and upper slopes of the ridge, but at some points extends right down into the valleys (cf. p. 153 and the map). This is also true of other parts of the Hindhead Common, not included in the map (owing to their survey not being complete). Where the C U facies extends down into the valleys, an investigation of the soil has failed to show any difference from that inhabited by the adjacent C U E facies.

(ii) If the two facies were due to the difference of habitat, one would expect to find a gradual transition between them, since the conditions of the habitat do not change suddenly. As it is however there is a very sudden change from the C U E to the C U, so sharp that it can easily be seen half-a-mile away (cf. Pl. V, figs. 1 and 2, and p. 154). We have no doubt that this sharp line of demarcation marks the limit of a fire, since the recent fires have left just such a line at other points on the area.

(iii) The *Calluna* and *Ulex* in the C U facies are much older (10-14 years) than the *Calluna* and *Ulex* in the C U E (about 5 years old).

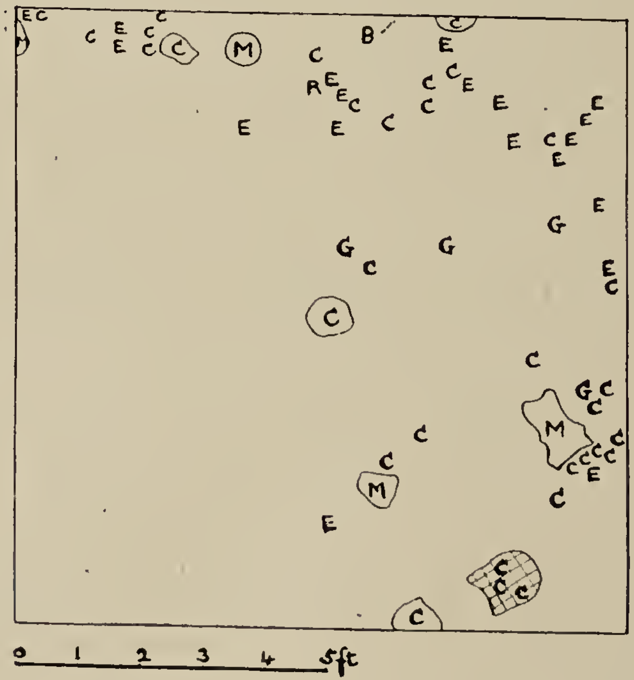
We think that these objections are sufficiently strong to make it very unlikely that the two facies are due to habitat or soil-conditions, and that they constitute good presumptive evidence for the view that the C U facies is merely a later stage of the C U E facies. Direct evidence is of course at present not obtainable, nor is it possible to say exactly how the transition is accomplished, But it appears probable that the dense branching of older *Calluna*-plants has a great deal to do with the elimination of the other constituents of the C U E facies. It may be recalled (p. 153) that where there is a break in the continuity of the *Calluna* on the ridge-top *Erica* and *Vaccinium* very often occupy the ground, and this tends to show that the habitat is quite suitable, but that these forms can only get on where they can escape the dense shade of the tall *Calluna*. As our observations progress year by year we hope to be able to collect the direct evidence, that will completely establish the correctness of the above view.

To summarise the preceding remarks we would distinguish the following four successive stages in the recolonisation of burnt ground on the heath at Hindhead. (a) Sprouting of the gorse. (b) Appearance of new growth from the base of other members of the heath-flora and development of a number of seedlings (gorse dominant). (c) *Calluna*, *Erica cinerea*, *Ulex minor* and to some extent *Pteridium* and *Vaccinium* competing for dominance (C U E facies). (d) *Calluna* (tall) and *Ulex minor* dominant, all other forms subsidiary (C U facies). Judging by the number of annual rings it would appear that the gorse-plants in the low and high *Calluna*-zones are almost invariably a year older than the corresponding *Calluna*-plants—an observation which indicates that also in these regions of the heath the gorse has been the first coloniser.

A word may be added on the behaviour of *Ulex minor* during the recolonisation of burnt ground. The shoots that arise from the old plants are at first all procumbent (Pl. V, fig. 4), but already during the first season following a fire upright branches appear on some of the plants. These upright branches however appear to grow but slowly in the first years, and it is only when *Calluna*, *Erica* and other forms are growing up all round that some of these upright shoots of the gorse begin to grow more vigorously and develop into the upright branches, described on p. 152. It is probably only those upright shoots that do not project far beyond the level of the surrounding heath that manage to survive the drying influence of the winds and that remain as upright shoots in the C U facies.

It is a familiar fact that after a heath-fire bracken often tends to appear in far larger quantity (cf. footnote on p. 158). As regards the area burnt in 1911, which bore very little *Pteridium* before the fire, there is some slight evidence of increase, but no very decisive proof can be adduced at present. The area burnt in 1909 lay largely within the zone in which bracken is a dominant, but here again we have hitherto failed to obtain any really decisive evidence of a marked increase. It may be pointed out that owing to the rapidity with which *Ulex minor* recolonises the ground, the bracken may not obtain those facilities for spreading its domain, which it finds on heaths not so largely occupied by gorse. We hope to be able to give further data on this point in later communications.

On the south-eastern slopes of the central ridge leading down to the valley B a number of land-slides have occurred some years back, whereby considerable stretches of yellow gravel of a rather coarse character have been exposed. This gravel extends to a depth of about four inches, being followed by grey sand with stones. On this gravel-area are large patches of the C U facies that have slipped down bodily from above and grow on stretches of soil like that on the ridge-top. Some of these patches consist of pure C U, while on others *Erica cinerea* flourishes extensively; the latter are no doubt derived from more open parts of the C U facies, in which the *Erica* had managed to hold its own, and now on an isolated patch, removed from competition with the *Calluna*, exhibits a more extensive development. Between these patches there are large areas of exposed gravel, the recolonisation of which is very slowly proceeding, and a study of the process has proved interesting in comparison with the colonisation of the burnt areas on the heath. On the gravel everything depends on the success of seedlings. The vegetation is at present very open, large areas bearing little or no growth. Part of the gravel is being colonised by *Molinia*, large plants of which are very abundant at some points and act as a kind of sand-binder (Pl. V, fig. 3). At other spots numerous seedlings and young plants of *Erica cinerea*, *Calluna* and *Molinia* are found, whilst *Ulex* is relatively much less important (cf. Text-fig. 4). A considerable number of seedlings of *Rumex* occur. The seedlings of all these forms do not appear to make much progress, and it is evident that, except for the *Molinia*, colonisation goes on very slowly.



Text-fig. 4. Chart to show recolonisation on exposed gravel; April, 1912. The cross-hatched area marks a patch of *Ulex minor* in which three *Calluna* seedlings have developed. M, *Molinia*; E, seedlings of *Calluna*; C with an enveloping line, *Calluna* plants; G, young grasses (in part *Molinia*); R, seedlings of *Rumex*; B, a small patch of moss (undetermined).

It is even now apparent that the vegetation, which will finally become established on the gravel, will bear a decidedly different aspect, at any rate for some time, to that on other parts of the heath; the Ericaceous forms (particularly *Erica*), as well as *Molinia*, will first be dominant, the gorse probably quite subsidiary.

In conclusion we should like to acknowledge our indebtedness to Mr. A. G. Tansley for much helpful criticism.

July, 1912.

EXPLANATION OF PLATE V,

ILLUSTRATING PAPER BY PROFESSOR FRITSCH AND MISS PARKER ON "THE HEATH ASSOCIATION ON HINDHEAD COMMON."

Fig. 1. End of central ridge, seen from a point corresponding approximately to the letter N in the right-hand lower corner of Text-fig. 1. The top of the ridge is occupied by the C U facies, which is separated by a sharp line from the C U E facies lower down. The vegetation in the foreground belongs to the slopes on the opposite (north-west) side of valley B.

Fig. 2. Line of separation of C U and C U E facies on the north-west side of the central ridge.

Fig. 3. Exposed gravel on south-eastern slopes of central ridge, partly occupied by *Erica cinerea* and *Molinia*. In the background extensive patches of C U, which have slipped down from the ridge above, are visible. The edge of the ridge is seen on the horizon.

Fig. 4. Burnt patch (burnt 1911), first year growth of *Ulex*. July, 1912.

Fig. 5. Burnt patch (burnt 1909). *Ulex minor* regenerating on burnt ground and infested by *Cuscuta*.

(Figs. 2, 3, 4 from photographs by Mr. W. B. Johnson; the rest from photographs by F. E. Fritsch.

ON VARIOUS METHODS FOR DETERMINING OSMOTIC PRESSURES.

With a Description of the Application of Barger's Method of Determining Molecular Weights to the Estimation of the Osmotic Pressure of the Cell Sap of Plants.

By A. C. Halket, B.Sc.,

Demonstrator in Botany, Bedford College, London.

[With Two Figures in the Text.]

I.—Some Methods of Determining Osmotic Pressure.

VARIOUS methods of determining osmotic pressure have been used at different times by workers investigating the properties of solutions of different kinds. A brief review of these may be useful.

1. *Plasmolytic method.* This method, which we owe to de Vries, has been the one generally employed to determine the value of the osmotic pressure of the cell sap of plants. Cells of the tissue under examination are placed in salt solutions of various known strengths and, as the solution which has exactly the same osmotic pressure as the cell sap causes no change to take place, that solution which causes just a slight shrinking of the protoplasm away from the cell wall is taken as isotonic (isosmotic) with the cell sap. This method is, however, not without its difficulties. Ewart[1] comments on this point in his paper "On the Ascent of Water in Trees," where he speaks of its want of exactitude for determining the osmotic pressure of the sap of small cells.

Some of the recent work on the toxic action of many of the common inorganic salts on the protoplasm of plant cells shows that plasmolysis of cells is induced by salt solutions of concentrations far weaker than those isotonic with the cell sap. Osterhout[2] reports that in young plants of *Vaucheria*, produced from zoospores, the protoplasm contracted away from the cell-walls when the filaments were immersed in a ·0937 gram-molecular solution of sodium chloride. Contraction of the protoplasm was also caused by a solution as dilute as ·0001 molecular if it was allowed to act for some days. This contraction was found not to take place if the salt solution was "balanced" by the addition of a little calcium chloride. Osterhout therefore suggests that the salt, sodium chloride, has some effect on the protoplasm which is not purely osmotic. True's[1] work on the physiological action of sodium chloride and potassium nitrate on *Spirogyra* cells also showed that these salts were not without some toxic action on protoplasm.

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[1] "On the Ascent of Water in Trees." Phil. Trans. Roy. Soc., Vol. 199, 1908, p. 355.

[2] "On Plasmolysis." Bot. Gaz., Vol. 46, 1908, p. 54.

2. *Direct determinations.* The osmotic pressure of various solutions has been measured *directly* by means of a semi-permeable or differential membrane of copper ferro-cyanide, first by Pfeffer, more recently by Morse and Fraser[2] and others, and by Berkeley and Hartley.[3]

3. *Indirect determinations.* The value of the osmotic pressure of any solution is, however, generally determined *indirectly* by utilising some other function of the solution which also depends on the amount of substance in solution. The osmotic pressure, the vapour pressure, the freezing point, and the boiling point are all functions of any solution which vary with its concentration, and the osmotic pressure has been calculated (*a*) from the difference between the vapour pressure of the solution and that of the solvent (*b*), from the depression of the freezing point of the solution below that of the pure solvent, and (*c*) from the elevation of its boiling point above that of the pure solvent.

4. *Physiological methods.* Certain physiological methods have been used to estimate the value of the osmotic pressures of various solutions.

The action of salt solutions on the red corpuscles of blood has been utilised to find what strengths of the solutions are isotonic. This has been done in two ways; the concentrations of different solutions that cause "laking" of blood have been compared, and the amount of decrease in volume of the corpuscles in different salt solutions has been measured by means of the hæmatocrit, and compared.

The behaviour of certain bacteria in various salt solutions has also been used to determine what concentrations of these solutions are isotonic.

As far as I know the majority of these methods have not been used for any extensive determinations of the osmotic pressure of the cell sap of plants. The great objection that can be brought against most of them is that a considerable quantity of liquid is required and this is difficult to obtain from many parts of plants. However, by one of the indirect methods mentioned above, utilising another physical property, osmotic pressures of cell sap have been determined.

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[1] "The Physiological Action of certain Plasmolysing Agents." Bot. Gaz., Vol. 26, 1898, p. 407.

[2] Amer. Chem. Journ., 1905-1909.

[3] Phil. Trans. Roy. Soc., Series A, 1906.

Freezing point method. In these cases the osmotic pressure of the cell-sap has been calculated from the amount the freezing point of the sap is depressed below that of pure water. The ordinary Beckmann's thermometer generally used to measure these small differences in temperature is large and so necessitates the use of a considerable quantity of sap—10-c.c. to 20-c.c. A smaller form of thermometer requiring only 1·5-c.c. of liquid has been described by Guye and Bogdan.[1]

Sutherst,[2] seeking to account for the fact that plants were not always injured by frost, found the depression of the freezing point of the sap of certain plants below that of pure water. He used somewhat watery plants, *e.g.*, vegetable marrow, celery, cabbage, etc., reduced the tissues to a pulp by means of a grater and obtained the sap by filtering the mass. He found the freezing point using 5-c.c. of the sap and a freezing mixture of Glauber salts and concentrated hydrochloric acid. He did not, however, calculate the values of the osmotic pressures of the various saps.

Atkins[3] gives a number of determinations of the values of the osmotic pressures of the sap of many fruits, tubers, etc., calculated from the depression of the freezing point found, using Beckmann's thermometer.

Cavara[4] has also made an extensive series of estimations of the osmotic pressure of the cell sap of the stems, leaves and fruits of many plants making the amount of the lowering of the freezing point the basis for calculating the osmotic pressures.

Dixon and Atkins[5] have described a modification of this method in which the change in the freezing point is measured, not by a thermometer, but by means of a galvanometer. The form of apparatus used requires 2·5-c.c. to 5-c.c. of liquid. The authors used their method to estimate the osmotic pressure of the expressed sap of the leaves of a number of trees. Dixon[1] has also estimated the osmotic pressure in leaves by placing shoots in a closed vessel containing some gas under high pressure and observing the pressure at which the leaves collapsed, *i.e.*, he found an external gas-pressure which balanced the internal pressure in the cells.

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[1] "Méthodes rapides pour l'analyse physico-chimique des liquids physiologiques." Journ. Chim. Phys., 1903.

[2] "The Freezing Point of Vegetable Saps and Juices." Chem. News Vol. 84, 1901, p. 234.

[3] "Cryoscopic Determination of the Osmotic Pressures of Some Plant Organs." Proc. Roy. Dub. Soc., Vol. 12, 1910; also Notes from the Bot. School Trin. Coll. Dub., Vol. 2, 1910.

[4] "Risultati di una serie di ricerche crioscopiche sui vegetali." Contrib. Biol. Veg., Vol. 4, 1905, p. 41. (Abstract in Bot. Centr., Band 104, 1907, p. 547).

[5] "On Osmotic Pressures in Plants, and on a Thermo-Electric Method of Determining Freezing Points." Proc. Roy. Dub. Soc., Vol. 12, 1910; also in Notes from the Bot. School Trin. Coll. Dub., Vol. 2, 1910.

II.—APPLICATION OF BARGER'S METHOD OF DETERMINING MOLECULAR WEIGHTS TO THE ESTIMATION OF THE OSMOTIC PRESSURE OF THE CELL SAP OF PLANTS.

In view of the fact that all the purely physical methods of determining the osmotic pressure of the cell sap of plants hitherto employed require a comparatively large amount of cell sap or somewhat elaborate apparatus, I thought it would be of interest to put on record a method I have used to determine the osmotic pressure of the cell sap of certain salt marsh and other succulent plants.

The method is a vapour pressure one and was invented by Barger[2] for estimating the molecular weights of small quantities of organic substances. The vapour pressure of the solution of unknown strength is compared with those of solutions of known strength. The vapour pressure of any solvent is lowered by the addition of any substance, and the amount by which it is lowered is proportional to the weight of substance present. As the osmotic pressure of any solution depends also on the amount of substance in solution and increases according to the amount of substance dissolved, the osmotic pressure of any solution varies inversely as the vapour pressure.

Barger states in his paper that the idea originated from an observation made during some experiments, on the adaptation of fungi to salt solutions, carried out in the late Professor Errera's laboratory in Brussels. The fungi were grown in hanging drops of solutions, the sides of the damp chambers being of cardboard kept moist with distilled water. The drops of solution were found to increase in size. This increase in size was explained by Professor

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[1] "On the Osmotic Pressure in the Cells of Leaves." Proc. Roy. Irish Acad., Ser. 3, Vol. 4, 1896, p. 61.

[2] "A Microscopical Method of Determining Molecular Weights." Trans. Chem. Soc., Vol. 85, 1906, p. 287.

Errera to be due to the fact that, as the vapour pressure of the salt solution was lower than that of water, the water vapour in the air of the damp chamber condensed more quickly on the surface of the hanging drop, the stronger solution. The drop therefore increased in size at the expense of the water in the cardboard. Barger investigated the phenomenon quantitatively and found that the best way to estimate the amount of change that took place in the volumes of any two solutions was to put drops of the solutions in a capillary tube and measure their increase or decrease under a microscope.

The vapour pressure of the cell sap is compared with that of each member of a series of salt solutions of which the concentration is known. These salt solutions differ only slightly in strength one from another, so that there is one whose vapour pressure will be approximately equal to that of the cell sap, the solution under investigation. When such a solution is found it is regarded as isotonic with the cell sap. The difference in vapour pressure of the two solutions, the cell sap and one of the solutions of known strength, is found by measuring the increase or decrease in the size of the drops of the solutions in a capillary tube.

Capillary tubes about three inches in length are used, and are filled as follows. One end of the capillary tube is closed by one's finger and the other end is dipped into the solution of known strength and a drop is allowed to run up the tube. The tube is then removed from the solution and a bubble of air is made to enter it, and it is then placed in the cell sap and a drop of that is allowed to run up, then another bubble of air, then another drop of the solution of known strength and so on. The process is repeated until the tube contains a number of drops of the two solutions alternating with each other, each drop being separated from the one next to it by a bubble of air. The size of the drops is regulated by pressure of the finger on the top of the tube. The first and last drops, which should be of the solution of known strength, are made much larger than the others. The number of drops is immaterial and is a matter of convenience. When there are a sufficient number of drops in the tube, the ends are sealed up and the tube, for convenience in handling and identification, is fastened to a microscope slide either with Canada balsam or with soft sealing wax. Other tubes are filled with one of the different members of the series of salt solutions of known strength and the cell sap. The slide, when full of tubes, is placed in a Petri dish containing water; this makes measurement easier and keeps the temperature constant. Fig. 1 shows the arrangement of the tubes, the black drops represent the salt solution of known strength, those shaded, the cell sap.

In this way in each tube there are a number of small chambers full of air, the end walls of each chamber being made by the surfaces of the two solutions. Evaporation of the solvent takes place from both surfaces into the closed air space, but condensation takes place more rapidly on the surface of the stronger solution. The drops of the stronger solution therefore increase in length while those of the weaker decrease.

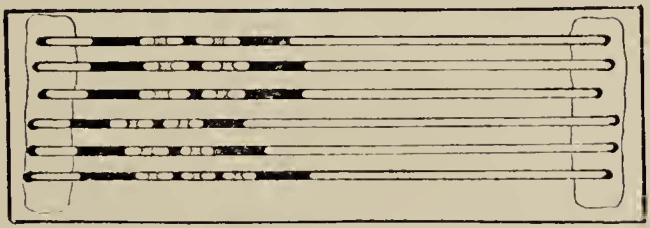

Fig. 1. For description see text.

As soon as the tubes are ready the lengths of the drops are measured. The first and last drops are not measured as their concentration may have been slightly altered when the ends of the tube were sealed. The drops are measured, under a low objective ($\frac{2}{3}$ inch) of the microscope, by means of a micrometer eye-piece. The middles of the menisci of each drop are focussed clearly and the distance between them read off on the scale. The appearance of the drop and the scale is shown in Fig. 2.

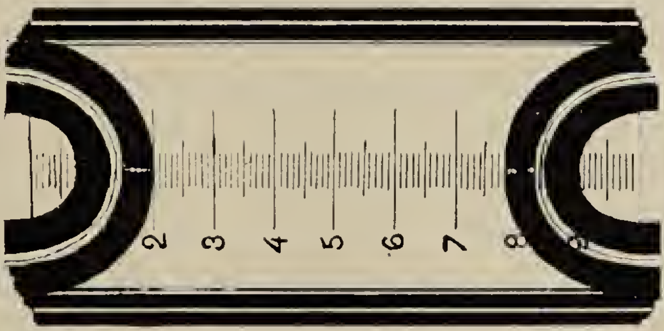

Fig. 2. For description see text.

The scale I used had 100 divisions. With care readings may be made to a tenth of one of these. Errors in reading were found not to exceed a fifth of one of the divisions.

After the drops are measured the tubes are set aside for some time. After an interval the drops are re-measured and the difference in length found. If the tubes have been carefully filled it will be found either, that in one tube of the series no change takes place in the size of the drops, or, as most frequently happens, that the drops of the cell sap increase in size when in tubes with solutions above a certain strength, while they decrease in size when with solutions below that strength. In the first case the solution with which no change takes place in the size of the drops is taken as isotonic with that of the cell sap. In the second case the mean between the known solutions, in the two tubes, is regarded as isotonic. Reference must be made to Barger's paper for further discussion of the method.

I first estimated the osmotic pressure of the cell sap of plants in this way while with Professor F. W. Oliver's expeditions to the Bouche d' Erquy in Brittany. During the course of the work there it was thought desirable to investigate the value of the osmotic pressure of the cell sap of some of the characteristic plants. The The greater part of the work was done on *Salicornia*. This is a very succulent plant, with a jointed stem and small opposite scale leaves. Underneath the epidermis there are two or three layers of small-celled palisade tissue, then a zone of aqueous tissue before the central strand with the vascular tissue is reached. The osmotic pressure of the cell sap was first estimated by plasmolysis, but this method was found to be satisfactorily applicable only to the cells of the epidermis and not to the cells of the aqueous tissue which are large and have no easily visible protoplasmic lining. It was therefore suggested by Mr. F. Baker, a chemist attached to the party, that it might be possible to use Barger's method for determining molecular weights in order to find the values of the osmotic pressure. The method was tried and found to be quite applicable, and many estimations were made.

Efficiency of Method. It was necessary to test the delicacy of the method, so a series of experiments was made to find whether the difference in the vapour pressures of solutions of sodium chloride in water, differing only slightly in strength, was sufficient to make the drops in the capillary tubes show any change in length. The solutions of salts generally used for the plasmolytic method vary in strength by ·01 of a gram-molecular solution. It was found that similar differences in strength could be detected by Barger's method. This is shown by the figures given below :—

Figures Obtained Using Two Solutions of Sodium Chloride Differing From Each Other by ·01 of a Gram-Molecular Solution.

G.-Mol. Strengths of Solutions	(*a*) 1st Reading. (*b*) 2nd Reading.	Lengths of Drops.				
1·59 & 1·58	(*a*)	78·0	65·0	55·5	84·4	48·5
	(*b*)	75·5	66·0	55·0	85·5	47·0
	Change	—	+	—	+	—
1·44 & 1·45	(*a*)	57·9	55·4	66·0	74·3	74·5
	(*b*)	58·3	54·9	66·8	74·0	75·1
	Change	+	—	+	—	+
1·43 & 1·44	(*a*)	77·5	93·4	71·0	84·4	80·7
	(*b*)	78·8	92·3	71·1	83·3	82·2
	Change	+	—	+	—	+
·2 & ·19	(*a*)	52·7	57·8	52·8	62·2	61·5
	(*b*)	51·9	58·5	52·1	63·0	60·8
	Change	—	+	—	+	—
·19 & ·18	(*a*)	62·2	41·4	45·9		
	(*b*)	61·5	42·2	44·9		
	Change	—	+	—		
·18 & ·17	(*a*)	47·7	52·5	74·7		
	(*b*)	46·6	53·5	73·3		
	Change	—	+	—		
·13 & ·14	(*a*)	41·3	44·3	41·5	32·5	46·7
	(*b*)	42·0	41·1	41·8	32·3	47·2
	Change	+	—	+	—	+
·12 & ·13	(*a*)	43·4	55·1	53·7		
	(*b*)	44·3	54·3	55·1		
	Change	+	—	+		
·12 & ·11	(*a*)	38·2	36·3	39·5		
	(*b*)	37·7	36·9	39·3		
	Change	—	+	—		
·11 & ·10	(*a*)	57·5	49·8	54·0		
	(*b*)	56·9	50·1	53·8		
	Change	—	+	—		
·08 & ·07	(*a*)	27·8	33·0	42·3	46·1	34·7
	(*b*)	27·2	33·7	41·3	46·8	34·1
	Change	—	+	—	+	—

This table shows the results obtained by balancing eleven pairs of solutions. The range of the concentrations is considerable, but the members of each pair only differ by ·01 gram-molecular solution. In each case the change that takes place shows quite definitely which of the two solutions is the stronger. On consideration of the figures it will be observed that the size of the drops does not vary regularly, the drops do not increase and decrease by the same amount. The change is not quantitative, the result simply shows that the drops of the stronger solution increase in length while those of the weaker decrease. Experience has shown that in order to get this regularity of increase and decrease great care must be taken in filling the tubes. The drops must not be allowed to run up and down the tube during filling, for if they do so the solutions become mixed as there is always a film of liquid on the sides of the tubes. This mixing does not so much affect the change when the difference between the concentrations of the solutions is greater, but with small differences it prevents a satisfactory result being obtained. The time it is necessary to leave between the first and second readings also varies with the strength of the solutions used. If the solutions differ very much from each other in strength, two to three hours is all that is necessary, but if the solutions are nearly equal in strength, *e.g.*, ·12 and ·11 molecular solution, the tubes must be left for a longer time. It was generally found convenient to fill the tubes one day, measure the drops, then leave them all night and re-measure the drops the next morning.

Values of the Osmotic Pressures of Cell Sap Found by Barger's Method.

In the tables below are given certain values of the osmotic pressure of the cell-sap of some succulent plants obtained by this method.

Salicornia ramosissima (from water channel).

Gram-Molecular Concentration of NaCl.

1·0			1·1			1·2			1·3		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
38·0	42·9	+	15·8	19·1	+	35·1	34·0	—	18·0	15·6	—
75·0	69·8	—	40·0	38·9	—	38·0	39·0	+	35·8	36·8	+
27·8	34·7	+	26·1	28·3	+	21·9	20·0	—	18·9	16·4	—

The vapour pressure of the cell sap is less than that of a 1·1 gram-molecular solution of sodium chloride and greater than that of a 1·2 solution, therefore the osmotic pressure of the cell-sap is taken to be equivalent to that of a 1·15 gram-molecular solution of this salt, *i.e.*, to 45·6 atmospheres at 18°C.

Salicornia ramosissima (from higher ground).

Gram-Molecular Concentration of NaCl.

1·6			1·5			1·4			1·3		
1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.
16·3	15·2	—	21·3	20·5	—	17·4	19·7	+	23·9	24·4	+
30·8	31·2	+	33·8	34·7	+	47·5	46·7	—	53·4	52·7	—
13·2	10·4	—	25·2	20·6	—	25·8	30·3	+	11·3	11·7	+
									61·2	60·6	—
									24·1	24·6	+

Therefore the osmotic pressure of the cell sap is taken to be equivalent to that of a 1·45 molecular solution of sodium chloride, *i.e.*, to 56·53 atmospheres.

Cotyledon sp.

Gram-Molecular Concentration of NaCl.

·15			·14			·13			·12			·11		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
58·7	55·2	—	65·3	63·5	—	79·8	80·9	+	54·3	56·2	+	68·4	69·8	+
72·2	75·6	+	87·3	88·9	+	55·4	54·8	—	54·7	52·4	—	47·1	44·6	—
63·2	58·7	—	89.0	87·2	—	48·0	48·3	+	53·5	56·5	+	52·6	55·2	+
87·6	90·0	+	82·6	84·6	+	38·4	37·5	—	63·4	61·8	—	70·1	67·5	—
50·7	47·9	—	74·2	72·1	—	58·4	59·3	+	58·2	59·8	+	35·4	37·1	+

Osmotic pressure of cell sap is therefore equivalent to that of a ·135 molecular solution of sodium chloride, *i.e.*, to 5·9 atmospheres.

Clinia nobilis.

Gram-Molecular Concentration of NaCl.

·10			·09			·08			·07			·06		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
73·4	71·3	—	56·9	54·8	—	26·0	27·2	+	14·7	15·5	+	52·0	54·0	+
67·1	68·6	+	59·7	59·9	+	51·4	51·1	—	59·5	58·7	+	98·8	95·6	—
83·8	82·6	—	35·3	35·1	—	20·6	20·8	+	51·1	51·3	—	76·8	78·6	+
56·7	57·6	+	73·9	74·1	+	42·0	41·9	—	49·5	48·7	—	43·4	41·5	—
61·8	59·6	—	27·8	27·6	—	75·2	75·4	+	47·2	47·4	+	44·8	46·8	+

The osmotic pressure of the cell sap is equivalent to that of a ·085 gram-molecular solution of sodium chloride, *i.e.*, is equal to 3·7 atmospheres.

Phyllocactus sp.

Gram-Molecular Concentration of NaCl.

·10			·09			·08			·07			·06		
1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
69·3	68·4	—	66·0	64·9	—	70·8	72·4	+	40·2	40·5	+	34·7	36·0	+
83·8	84·6	+	71·4	72·2	+	94·4	93·4	—	73·3	72·8	—	68·5	68·2	—
56·2	55·2	—	40·7	39·9	—	51·3	55·0	+	29·2	29·6	+	61·2	62·9	+

Therefore the osmotic pressure of the cell sap is equal to that of a ·085 molecular solution of sodium chloride, *i.e.*, to 3·7 atmospheres.

Cereus sp.

Gram-Molecular Concentration of NaCl.

·14			·13			·12			·11			·10		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
57·6	55·8	—	48·7	47·5	—	53·1	52·3	—	34·6	35·1	+	58·2	59·5	+
64·0	65·3	+	84·6	85·0	+	86·3	86·6	+	93·1	92·8	—	75·0	74·4	—
36·3	35·1	—	91·7	91·1	—	66·1	65·3	—	53·7	53·9	+	62·3	63·3	+
51·3	52·3	+	63·2	63·7	+	74·0	74·3	+	52·0	51·3	—	52·5	51·5	—
33·0	31·7	—	59·7	59·6	—	63·5	63·0	—	20·7	21·2	+	43·0	43·4	+

Osmotic pressure of cell sap taken to be same as that of a ·115 molecular solution of sodium chloride, *i.e.*, to be 5 atmospheres.

Crassula lactea.

Gram-Molecular Concentration of NaCl.

·09			·08			·07			·06			·05		
1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.	1st Reading.	2nd Reading.	Change.
65·7	64·2	—	33·0	32·7	—	59·4	57·5	—	75·9	76·6	+	37·5	37·9	+
55·9	56·9	+	55·2	55·4	+	82·0	83·2	+	63·3	61·7	—	57·6	56·9	—
74·4	72·9	—	60·8	61·3	—	53·2	51·3	—	57·7	60·0	+	60·8	61·1	+

Osmotic pressure of sap equals that of a ·065 molecular solution of sodium chloride, *i.e.*, is equal to 2·9 atmospheres.

On examining these results it will be seen that there is a considerable range of pressures obtained for the different plants. The osmotic pressure of a plant of *Salicornia ramosissima* from the high ground of the marsh was found to be much greater than that of a plant from a depression on the marsh. The same values had previously been obtained by plasmolysis of the epidermal cells; when some of the plants examined from the higher parts of the marsh were found to have a cell sap isotonic with that of a 1·45 gram-molecular solution of sodium chloride while many of those from the lower parts had cell sap isotonic with that of a 1·15 solution. These values are high but they lie between the limits subsequently observed by Fitting[1] who found that the cell sap of plants of *Salicornia herbacea* from a very damp and salt habitat had cell sap of an osmotic pressure greater than that of a 1-gram-molecular solution and less than that of a 2-gram-molecular solution.

The strength of the cell sap of *Cereus* sp. found by Barger's method is in accordance with that found by Livingston[2] for a species of *Cereus*. He determined the osmotic pressure of the sap in two ways:—(i) by finding the depression of the freezing point which gave a pressure equal to that of 5·5 atmospheres, and (ii) by observing the change in curvature of "strips" of tissue placed in salt solutions of various strengths, when the pressure was found to vary from 3·9 to 7 atmospheres in different plants.

The values obtained for the other plants are somewhat lower than those generally expected for plant cells, but they are not so low as some recorded for other succulents. Cavara[3] estimates the osmotic pressure of the sap of *Aloë arborescens* to be equal to a pressure of 1·5 atmospheres.

The advantages which Barger's method has over other physical methods that have been tried for finding the osmotic pressure of the sap in plant cells, are twofold. In the first place a very small quantity of sap is sufficient to make a determination, so that the osmotic pressure of the cell sap of any small part of a plant, *e.g.*, a single leaf, can be estimated. This is necessary when it is desired to correlate the osmotic pressure of the cell sap of leaves, with age of leaf as done by Pringsheim[4] for certain succulent plants, or with any special factor in the life of the plant. The juice of the organ can be squeezed out by pressure of the fingers and the drops obtained can be used directly to fill the tubes. In the second place no elaborate apparatus is required,—the capillary tubes can easily be made by drawing out ordinary glass tubing.

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[1] "Die Wasserversorgung und die osmotischen Druckverhältnisse der Wustenpflanzen." Zeitschr. f. Bot., Band 3, 1911, p. 250.

[2] "The Relation of Desert Plants to Soil Moisture and to Evaporation." Carnegie Institute, Publication No. 50, 1906.

[3] Loc. cit.

[4] "Wasserbewegung und Turgorregulation in welkenden Pflanzen." Jahrb. f. wiss. Bot., Bd. 43, 1896, pp. 89-144.

There are, however, some disadvantages which must be considered. Firstly, the amount of time, which must be allowed to elapse between the two readings, is long. This is due to the low vapour pressure of water, the solvent used. It was generally found necessary to leave the tubes overnight to obtain a definite result. However, this length of time can be shortened by raising the temperature at which the drops are kept in the manner described by Barger and Ewins.[1] Secondly, the tubes require to be filled with great care, as the drops of the salt solution and of the cell-sap must not be allowed to mix on the sides of the tubes more than is unavoidable, a slight mixing being of course inevitable. With a little practice the tubes can be filled quite easily.

There is still another disadvantage which Barger's method has in common with the cryoscopic method and all others that deal with sap outside the cell. This is, it does not allow for any chemical changes that may take place and which might alter the osmotic strength of the sap. For this reason, Fitting[2] comments unfavourably on the use of the cryoscopic method. While working on *Salicornia* I estimated the osmotic pressure of the sap by plasmolysis and by Barger's method, and found that the results obtained in both cases varied between similar limits.

I wish here to express warm thanks to Professor F. W. Oliver, in whose laboratories part of this work was done, and to Miss E. N. Thomas for her kindness in reading and criticising the manuscript of this paper.

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[1] "Application of the Microscopic Method of Molecular Weight Determination to Solvents of High Boiling Point." Trans. Chem. Soc., Vol. 87, 1905, p. 1757.

[2] Loc. cit., p. 223.

RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

(Continued from p. 123*).*

FROM simple Cryptomonads—like *Protochrysis*, *Cryptochrysis*, or *Wysotzkia*—various diverging lines may be traced. One of these leads to the endozoic "Zooxanthella" forms; some at any rate of the "Zooxanthellæ" belong to the Cryptomonads and are placed by Pascher in a new genus, *Chrysidella*. Two other lines, marked by the fixation of the blue-green and the red chromatophores found sporadically in the simpler Cryptomonads, lead respectively to the blue-green genera *Chroomonas* and *Cyanomonas* and to the red genus *Rhodomonas*. Another line leads to *Cryptomonas* and *Nephroselmis*, with firm periplast, and from these have been derived the colourless forms *Chilomonas*, *Cyathomonas*, and *Oxyrrhis*. The fifth line has probably led to the Dinoflagellata (Peridiniales) on one hand, and through simple palmelloid types to the Phæocapsaceæ on the other. In the Phæocapsaceæ, beginning with simple gelatinous forms like *Phæoplax*, *Phæocystis*, and *Phæococcus*, we have a series of transitional types leading to the definitely filamentous *Phæothamnion* and so to the Ectocarpales.

The inter-relationships of the Brown Flagellate and Algal groups as here suggested are indicated on the accompanying scheme (Table C).

VIII.—The Peridiniales (Dinoflagellata) and their Relationships.

The Peridiniales, mainly marine but also found in fresh waters, and often forming a considerable part of the microplankton, are always unicellular and usually isolated, though sometimes cohering in chain-like colonies and in one family (Phytodiniaceæ) forming palmelloid aggregations by repeated division within gelatinous envelopes. There are typically two dissimilar flagella, usually lodged in grooves—one longitudinal and the other transverse—and in most cases the protoplasm is clad by a cellulose wall, typically built up of a series of sculptured and perforated plates. Oil is usually formed as the product of anabolism, even in forms possessing pyrenoid-like bodies, but in a few cases starch is produced. Most of the Peridiniales have yellow or brown or (in some freshwater species) green chromatophores, usually numerous and band or rod-like and radially arranged, but sometimes these are absent or represented by leucoplasts—these colourless forms are mostly saprophytic or in some cases holozoic, while Dogiel (41) and Chatton (21, 22) have recently shown that certain forms are parasitic on various animals. Reproduction takes place by division into two or more daughter cells (spores or zoogonidia) and resting cysts are also formed by rejuvenescence of the cell contents. However, the life cycle of very few forms has yet been worked out,

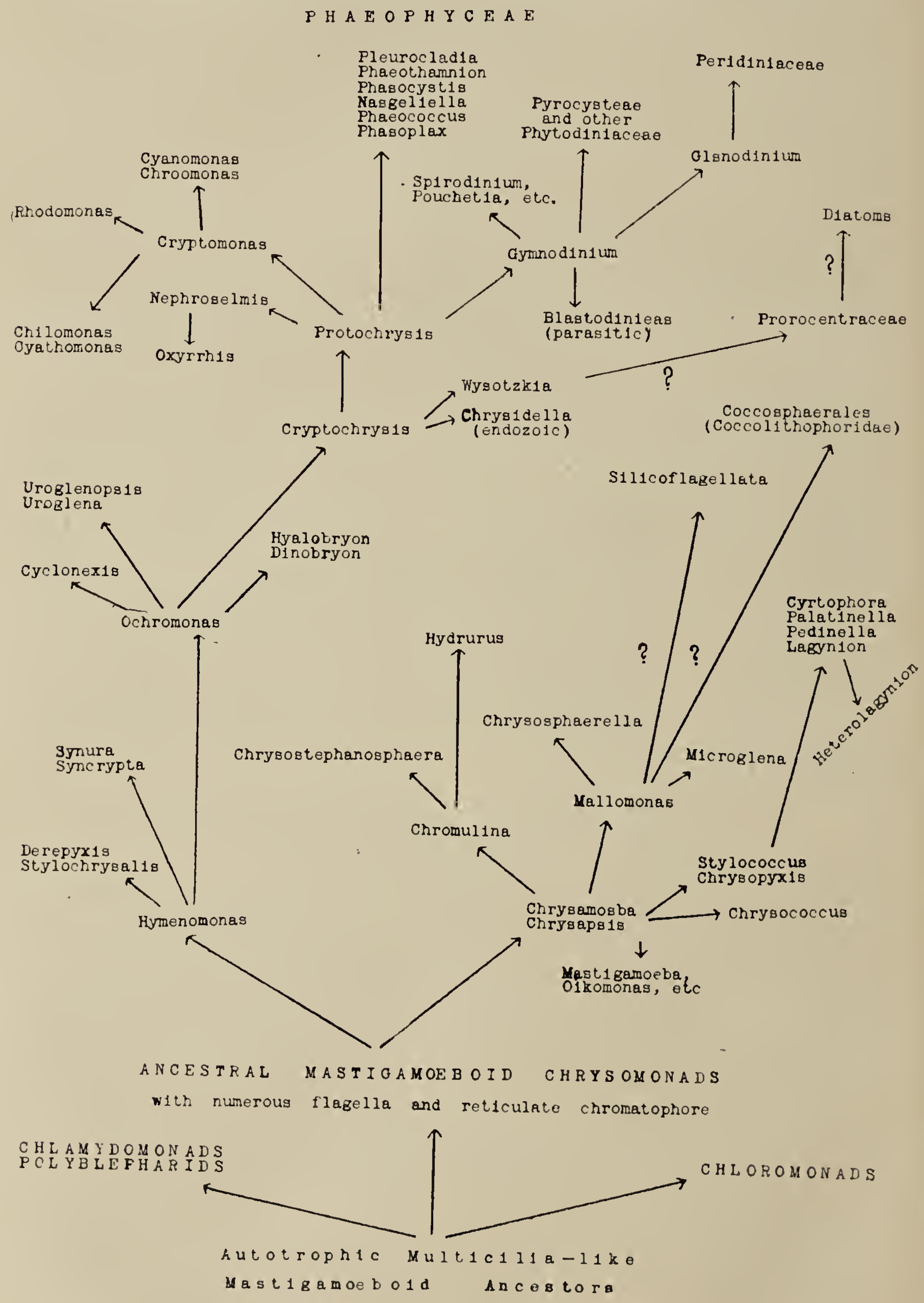

Table C.—Suggested Phylogeny of Brown Flagellate and Brown Algal Series. For details see Text.

despite the voluminous literature that has accumulated as the result of the collection of plankton Peridiniales, at all times of the year, by numerous workers; there is, for instance, no proof at present that a sexual process occurs in the group—unless we include in it the genus *Noctiluca* (see below). Zederbauer (157) observed individuals of *Ceratium Hirundinella*, a freshwater species, grouped in pairs and connected by protoplasm, while the contents of other individuals had been extruded in the form of a cyst—whence he inferred that zygospores had been formed as the result of a conjugation process. However, Jollos (62) and Wesenberg-Lund (145) observed the formation of similar cysts in *Ceratium* which had certainly arisen without copulation, and it would appear that the paired cells seen by Zederbauer had arisen as the result of abnormal cell division or that the process may be simply one of plastogamic fusion such as occurs in certain Protozoa.

Schütt (134) divided the Peridiniales into three families—Gymnodiniaceæ, Prorocentraceæ, and Peridiniaceæ. In the Gymnodiniaceæ the cell is naked or clad only by a thin mucilaginous or cellulose wall showing uniform structure and in most cases forming merely a delicate periplast like that of the majority of Flagellata. Of the two flagella, one is directed backwards in the longitudinal groove (sulcus) while the other (usually thrown into undulating curves) lies in the transverse groove (annulus). Both sulcus and annulus may be straight, meeting at right angles at one point where the flagella arise—in this case the annulus is either subequatorial (complete in *Gymnodinium*, a half-ring in *Hemidinium*) or is near the anterior pole so that the anterior (præ-annular) portion of the cell is much smaller than the posterior and is rostrum-like (*Amphidinium*); or the annulus may be spirally coiled and the sulcus slightly (*Spirodinium*) or markedly (*Cochlodinium*, *Pouchetia*) spiral also, meeting the annulus at both ends, with the transverse flagellum inserted at the anterior end of the annulus and the longitudinal flagellum at the posterior end of the sulcus—*Pouchetia* is distinguished from *Cochlodinium* by having a complicated stigmatic apparatus consisting of a red or black pigmented body with one or more large spheroidal refractive lens-like bodies adjoining it. In this family Schütt includes *Pyrocystis* (see below).

In the Prorocentraceæ (Fig. 8) there is a shell consisting of two biconvex valves, dotted with pores except on either side of the suture; from an opening in this suture, at the anterior end of the cell, arise the flagella, of which one is directed forwards while the second either vibrates about the base of the first or is directed laterally. In the three genera included here by Schütt, there are usually two large plate-like chromatophores, one lying within each valve of the wall, but sometimes these are deeply lobed or even divided into a number of radiating elongated chromatophores, as in the majority of Peridiniales. In *Cenchridium* the pore from which the flagella arise is continued inwards as a gullet-like tube; in *Exuviælla* and, more markedly, in *Prorocentrum*, there are small projections of the wall close to the flagellum pore, which Schütt suggests may represent the beginnings of the characteristic wing-like expansions of the margins of the flagellum groove in the Peridiniaceæ.

The remaining Peridiniales are placed by Schütt in the family Peridiniaceæ, in which the shell differs from that of the Prorocentraceæ in having a series of girdle plates intercalated between the two valves. The girdle consists essentially of a narrow ring-like plate with a groove (annulus) for the transverse flagellum, and a pair of plates (sometimes each divided into several plates) placed at right angles to this and containing the longitudinal groove (sulcus). Each valve consists of two or more polar plates, which are either joined directly to the girdle series or are separated by intercalary plates. The upper valve (epitheca) bears an apical pore, and in most cases the sulcus is confined to the lower valve (hypotheca), though sometimes it extends beyond the annulus right to the apex of the cell (*Steiniella*, *Gonyaulax*), or it may be short and extend equidistantly on either side of the annulus (*Protoceratium*). Schütt divides the Peridiniaceæ into four sub-families—Glenodinieæ (only genus *Glenodinium*); Ptychodisceæ (only genus *Ptychodiscus*); Dinophyseæ (six genera, including the most bizarre forms of

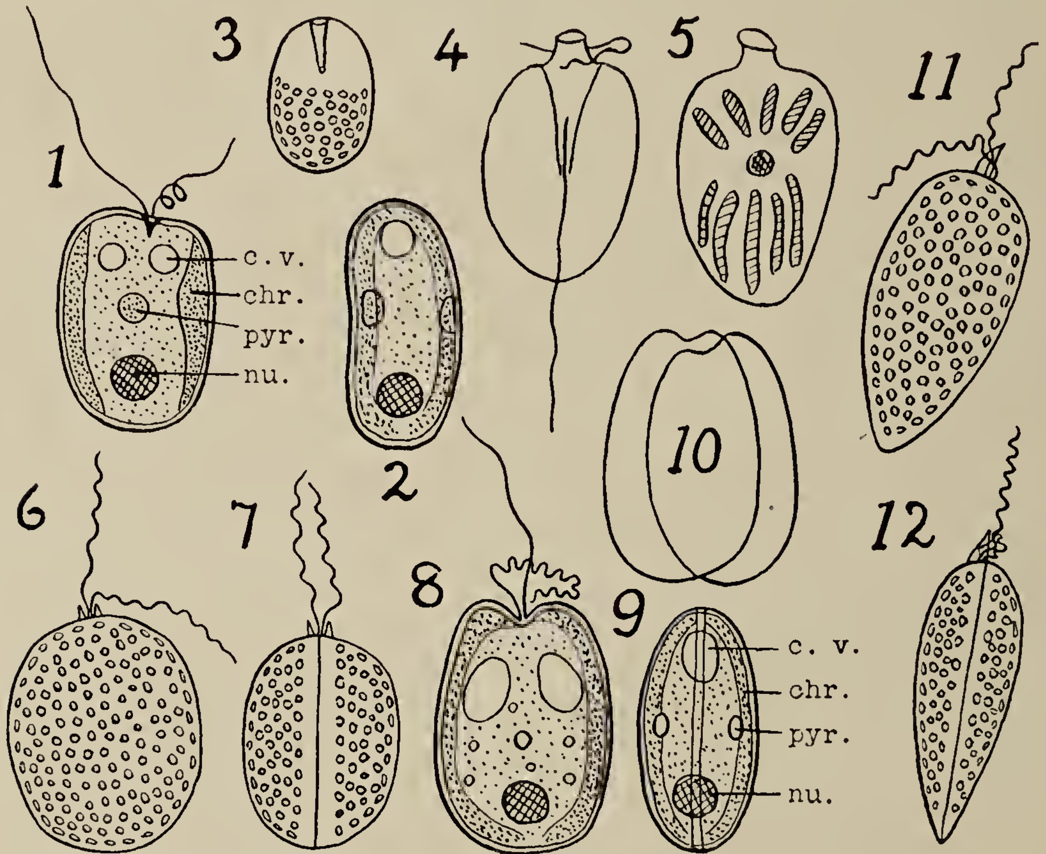

Fig. 8. Prorocentraceæ.—1, 2, *Haplodinium antjoliense* Klebs : 1, surface view ; 2, side view ; 3, *Cenchridium globosum* (Williams) Stein. 4, 5, *Amphidinium operculatum* Clap. et Lach. ; 4, ventral view, showing the flagella ; 5, dorsal view, showing nucleus and chromatophores. 6 to 10, *Exuviælla marina* Cienk. : 6 and 7, two aspects at right angles to each other, showing the flagella and the surface markings of the shell ; 8 and 9, optical sections corresponding respectively with 6 and 7, and showing the nucleus, chromatophores, pyrenoids, and contractile vacuoles ; 10, empty valves of the shell, after escape of encysted contents. 11 and 12, *Prorocentrum micans* Ehrb., two views at right angles. *Chr.*, chromatophore ; *c. v.*, contractile vacuole ; *nu.*, nucleus ; *pyr.*, pyrenoid.

1, 2, 8, 9, 10, from Klebs ; 3, 4, 5, from Stein ; 6, 7, 11, 12, from Schütt. All somewhat diagrammatic.

Peridiniales); and Ceratieæ (*Ceratium*, *Peridinium*, etc.—this is the largest division of the group). In the Dinophyseæ the shell is divided by a longitudinal suture into two subequal lateral portions the epitheca is much smaller than the hypotheca, the borders of the annulus are funnel-like and the left-hand border of the sulcus is often developed into wings and spines.

According to Schütt, the Peridiniaceæ are connected with the Gymnodiniaceæ by the genus *Glenodinium*, and with the Prorocentraceæ by the genus *Ptychodiscus*. In *Glenodinium* (Fig. 9, *9* to *13*) the shell is thin and structureless (not sculptured or perforated), and its differentiation into two valves and a girdle is only apparent when rupture occurs at liberation of the encysted contents. In *Ptychodiscus* the two valves have the same structure as in the Prorocentraceæ, but the girdle is represented by a thin soft membranous ring-like band, while the sulcus is indicated by a depression on one valve and a narrow plate on the other.

The results of recent work suggest considerable modifications of Schütt's classification of the Peridiniales, and appear to afford a basis for phylogenetic interpretations very different from those put forward by that author in 1896. Our knowledge of the Peridiniales and allied groups has been greatly extended in recent years by the work of Apstein (1, 2), Borgert (13), Chatton (21, 22), Dogiel (41), Jollos (62), Klebs (68), Kofoid (71, 72), Lemmermann (75–85), Lohmann (86-88), Schilling (127, 128), and others; the literature is cited by Pavillard (115) and in various other general works.

The view that the Peridiniales are related to the Flagellata appears to have been first put forward by Bergh (4), who pointed out the striking resemblances between *Prorocentrum* and the Cryptomonads. Bergh also suggested that a form like *Prorocentrum* might have given rise to the Dinophyseæ, in which the transverse groove is near the anterior end of the cell, and that the Ceratieæ are derived from the Dinophyseæ by progressive shifting backwards of this groove to an approximately median position. Bütschli (18), on the other hand, considered that in the evolution of the Peridiniales shifting of the annulus had taken place from behind forwards; according to his interpretation of the structure of *Prorocentrum*, which is followed by Schütt, the suture between the two valves is horizontal, and the insertion of the flagella lateral. Bergh and Bütschli agreed in regarding the simple shell-less Gymnodiniaceæ as derived by reduction from the typical shell-clad Peridiniales, and various other writers have adopted this view, as being a necessary consequence of the principle that the Peridiniales are of monophyletic origin.

A much simpler interpretation is obtained if we regard the suture in the Prorocentraceæ as being *longitudinal* and as corresponding with the longitudinal suture in the Dinophyseæ, which ought perhaps to be separated as a distinct family—the higher Peridiniales (Schütt's Peridiniaceæ) would then fall into two families, Ceratiaceæ and Dinophysidaceæ. Including the two families recently founded by Klebs and by Chatton, the Peridiniales as a whole may be regarded as forming two distinct series, which it is here suggested are of independent origin from the Cryptomonads.

The Gymnodiniaceæ (Fig. 9) may well have arisen from a Cryptomonad like *Protochrysis*, with two unequal flagella arising from a lateral depression having the form of an incomplete transverse groove. In the Gymnodiniaceæ, however, there are numerous chromatophores instead of two, and the nucleus, as pointed out by Klebs (68) has a characteristic fibrillar structure apparently not found in the Chrysomonadineæ. But granting these differences, and the absence of what may be strictly regarded as transitional

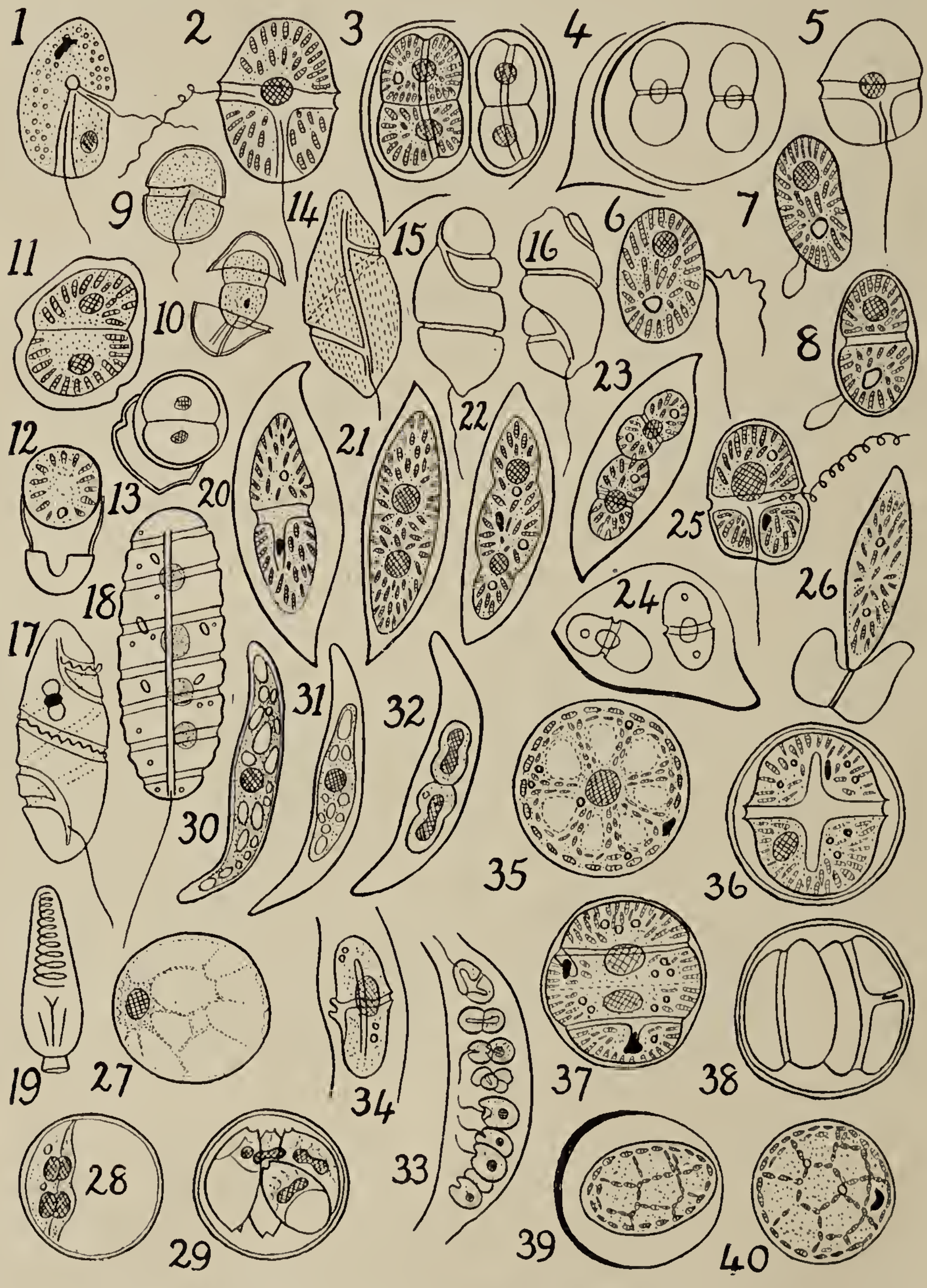

Fig. 9. Gymnodiniaceæ.—1, *Hemidinium nasutum* Stein, showing flagellum grooves, flagella, nucleus, and numerous small chromatophores. 2, *Gymnodinium bogoriense* Klebs. 3 to 8, *Gymnodinium rotundatum* Klebs: 1, two cysts enclosed in the membrane of the parent cell; 2, rupture of cyst shown on the left in preceding figure, to set free the two motile cells; 5, motile cell; 6, the

same gradually coming to rest and about to lose its flagella ; 7, the same after loss of flagella, secreting a drop of mucilage for attachment ; 8, the same, two days later (the transverse furrow which had disappeared on coming to rest has now been re-formed). 9, 10, *Glenodinium pulvisculus* Ehrb.: in 10 one of the shell-valves has been forced off to allow escape of the spore, which soon afterwards undergoes division. 11 to 13, *Glenodinium emarginatum* Klebs: in 11 the cell contents have undergone oblique longitudinal division; 12 shows escape of contents as a spore (cyst), and 13 the division of this cyst. 14, *Spirodinium spirale* (Bergh) Schütt. 15, 16, *Cochlodinium strangulatum* Schütt. 17, *Pouchetia fusus* Schütt, showing the spirally coiled flagellum grooves, and the stigma (consisting of a pigment-body with a refractive lens-like body on either side of it. 18, 19, *Polykrikos auricularia* Bütschli : in 18 the longitudinal flagellum groove, eight transverse grooves, four nuclei, and five trichocysts ; 19, a trichocyst. 20 to 26, *Cystodinium bataviense* Klebs : 20, cyst with Peridinean body ; 21 to 23, stages in division of cyst contents into two cells, which escape by gelatinisation of one side of the cyst (seen in 24) ; 25, motile cell ; 26, motile cell has become a cyst, set free by rupture of the cell-wall ; the black fleck in 20, 22, and 25 is a stigma ("eye spot"). 27 to 34, *Diplodinium lunula* (Schütt) Klebs (= *Pyrocystis lunula* Schütt) : 27, uninucleate primary cyst ; 28, cyst with four nuclei, the cytoplasm not yet divided ; 29, cyst with four cells, each about to divide again ; 30, sickle-shaped secondary cyst ; 31, contraction of contents of same ; 32, 33, division of contents into motile *Gymnodinium*-like cells, of which one is shown more highly magnified in 34. 35 to 40, *Hypnodinium sphæricum* Klebs ; 35, a cell in optical section, showing the central nucleus, the numerous small chromatophores in the peripheral and radiating portions of the cytoplasm, an "eye spot," and five orange-red oil drops ; 36, cell with rounded off contents showing *Gymnodinium*-like grooves ; 37, stage in division, showing two nuclei, two transverse grooves, and two "eye spots" ; 37, division into two *Gymnodinium*-like cells completed ; 39, 40, rupture of cyst, setting free the two daughter cells, which have now lost their grooves.

1, 9, 10, from Stein ; 2 to 8, 11 to 13, 20 to 26, 35 to 40, from Klebs ; 14 to 17, from Schütt ; 18, 19, from Bergh.

forms, there appears to be little doubt that the discovery of *Protochrysis* has at any rate lessened the gap between the Cryptomonads and a simple Peridinean genus like *Hemidinium* with its incomplete transverse groove. From a form like *Hemidinium*, the transition is easy to *Gymnodinium* and to *Glenodinium* (which is best placed in the Gymnodiniaceæ and which forms a connecting link with the Ceratiaceæ). These simple Gymnodiniaceæ form a central group from which diverge lines leading in various directions. In *Spirodinium*, *Cochlodinium*, and *Pouchetia* the cell is elongated and the grooves spirally coiled, and the pigmented body (stigma) found in the simpler forms is accompanied in *Pouchetia* by one or more lens-like bodies. In *Pouchetia armata* (Dogiel, 41) the cell is provided with nettling organs (trichocysts) consisting of a conical capsule containing a coiled stinging thread. Nettling organs of this kind are also found in the remarkable naked holozoic genus *Polykrikos* (Bütschli, 18 ; Kofoid, 72), in which the elongated body has eight transverse grooves and a single straight longitudinal groove, and there are eight nuclei—according to Delage (37) these are meganuclei, accompanied by smaller nuclei (micronuclei) as in Ciliate Infusoria, and each transverse groove has a flagellum. From Kofoid's account of *Polykrikos*, it would appear that the apparently single cell is a colony of individuals arranged in a linear series, owing to incomplete separation after division ; Dogiel (41) has described specimens with four transverse grooves and a single nucleus. *Polykrikos* may be definitely placed in the Gymnodiniaceæ, since the presence of nettling organs in *Pouchetia* connects it with *Cochlodinium* and *Spirodinium* and thus with the simpler genera like *Gymnodinium*. Whether *Polykrikos* forms a link between the Peridiniales and the Ciliate Infusoria is, of course, an open question in the absence of further transitional types. It is possible that the genus *Erythropsis* (Hertwig, 57; Delage, 37; Pavillard, 114) affords such a transition; in this organism the irregularly spherical body shows a longitudinal groove, a transverse groove with a wavy flagellum at the anterior end of the body, and a relatively thick contractile outgrowth at the posterior end, while there is a stigmatic apparatus comparable with that of *Pouchetia*. Hertwig regarded *Erythropsis* as an Infusorian allied to *Vorticella*; while Metchnikoff compared its appendage to the sucker of *Acineta* and placed the genus in the Suctorial Infusoria. It is probable that the resemblances to Infusoria presented by *Polykrikos* and *Erythropsis* are merely superficial or due to homoplasy; in any case, both genera appear to be directly related to the Gymnodiniaceæ.

The life cycle of the lower Gymnodiniaceæ, so far as known, is extremely simple. In some cases division occurs in the motile condition, but more usually after encystment, the cyst being covered by gelatinous envelopes or by a firm wall and its contents dividing into two or more cells. In *Cystodinium* (Fig. 9, *20-26*) the motile cells resemble *Gymnodinium* in structure, but on becoming encysted they acquire an elongated and horned form, the contents then become rounded off and dividing to produce two or four motile cells. In *Diplodinium* (Fig. 9, *27-34*) the life cycle is somewhat complicated, since the encysted cell divides to form sixteen secondary cysts, each of which gives rise to four, eight, or sixteen motile *Gymnodinium*-like cells; to this genus Klebs refers *Pyrocystis lunula* and certain species which had previously been placed in the genus *Gymnodinium*. Finally, *Hypnodinium* (Fig. 9, *35-40*) is known only in the resting stage; on becoming encysted, the protoplast shows *Gymnodinium*-like grooves and divides into two naked cells exactly like *Gymnodinium* but without flagella—on being set free by rupture of the cyst these two cells acquire a membrane and soon form new cysts.

In the genera *Blastodinium* and *Apodinium*, recently discovered by Chatton (21, 22), and perhaps best placed in a family (Blastodiniaceæ) distinct from but closely allied to the Gymnodiniaceæ, which live as parasites or commensals in the bodies of Copepods and other marine animals, the cell divides into two portions, of which one continues the ordinary vegetative cycle while the other divides into a number of cysts which are set free as biflagellate *Gymnodinium*-like cells.

The genus *Diplodinium* leads from the Gymnodiniaceæ to the family Phytodiniaceæ (Fig. 10, *1-13*), which includes the old genus *Pyrocystis* (minus *P. lunula*, now transferred to the genus *Diplodinium*) and four new genera founded by Klebs (68). In this family the cells show Peridinean cytological features, though no grooves are present; reproduction takes place by simple division of the cell contents into two, but no motile cells have been observed. The simplest form is *Phytodinium*, with ovoid cells (Fig. 10, *1, 2*); in *Pyrocystis* (Blackman, 8) the protoplasm is radially arranged, and is massed together at one end of the cell, very much as in the primary cyst of *Diplodinium lunula*; in *Tetradinium* (Fig. 10, *3-7*) the cell is tetrahedral, with two pointed processes at each angle; in *Stylodinium* (Fig. 10, *8, 9*) the oval or spherical cell is attached to a substratum by means of a gelatinous stalk; while in *Glœodinium*

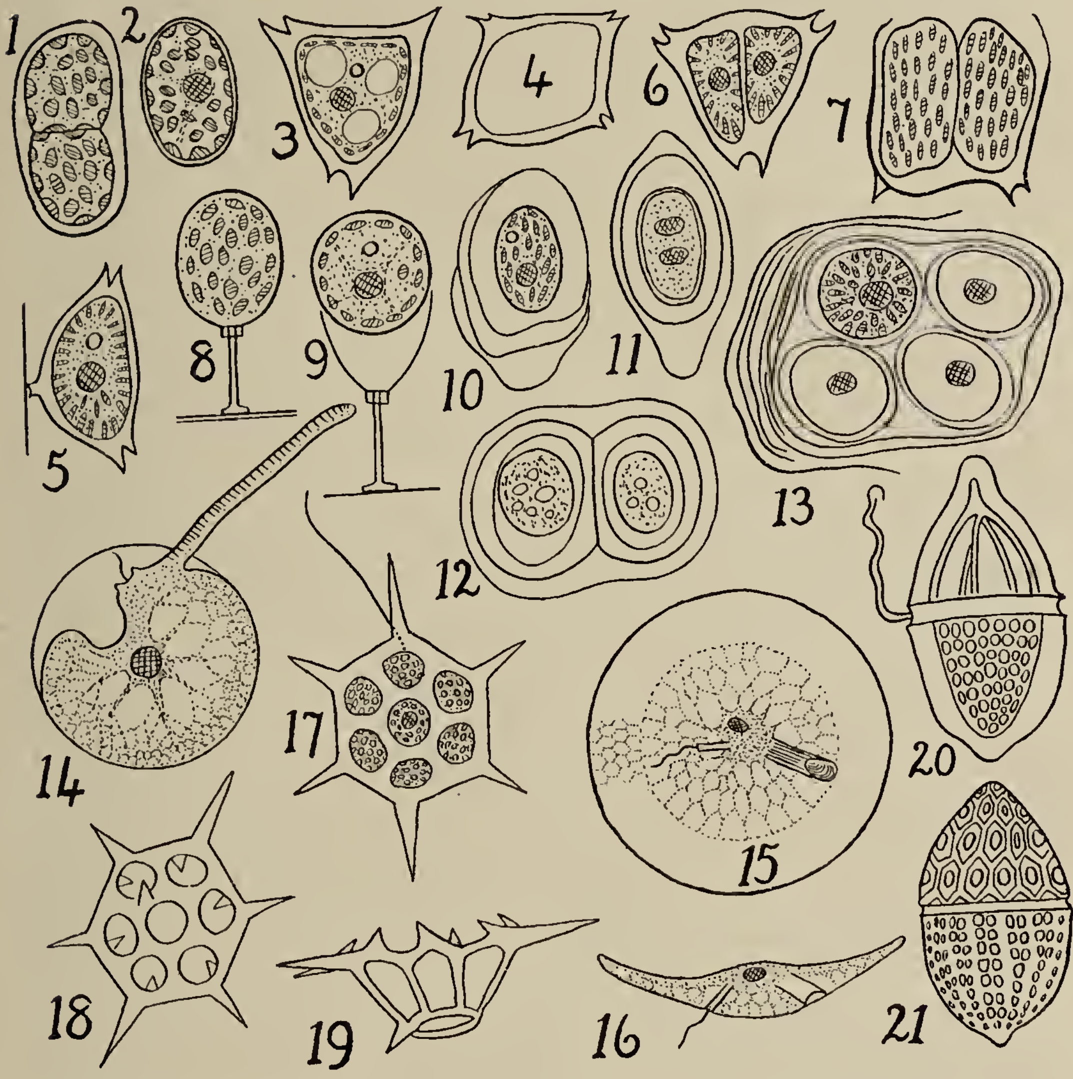

Fig. 10. PHYTODINIACEÆ (1 to 13), CYSTOFLAGELLATA (14 to 16), and SILICOFLAGELLATA (17 to 21).

1, 2, *Phytodinium simplex* Klebs: in 1 the cell has divided, in 2 the nucleus is shown. 3 to 7, *Tetradinium javanicum* Klebs: 3, cell showing vacuolate cytoplasm, nucleus, an oil-drop, and numerous peripheral chromatophores; 4, empty cell, showing all four angles; 5, cell attached to a root-hair of *Azolla*; 6, division; 7, escape of the two daughter-cells from ruptured cyst-wall. 8, 9, *Stylodinium globosum* Klebs: 8, stalked cell attached to a root-hair of *Azolla*; 9, escape of undivided contents by rupture of old cell-wall. 10 to 13, *Glœodinium montanum* Klebs: 10, cell with several gelatinous envelopes derived from older membranes; 11, division of the nucleus; 12, cell division; 13, older colony surrounded by gelatinous envelopes. 14, *Noctiluca miliaris* Suriray: side view (optical section), showing on the left the short flagellum inserted in the "pharynx," at the base of the thick tentacle. 15, 16, *Leptodiscus* Hertwig: 15, surface view, ventral side, showing on the right a wide depression with striated walls and on the left the narrow tube containing the flagellum; 16, side view (optical section). 17 to 19, *Distephanus speculum* Stöhr: 17, cell showing skeleton and cell-contents (nucleus, cytoplasm, chromatophores); 18, 19, two views of skeleton. 20, *Monaster rete* Schütt: side view, showing the two flagella arising from equatorial groove, and the internal skeleton. 21, *Amphitolus elegans* Schütt: side view, showing the elaborate skeleton.

1 to 13, from Klebs; 14 to 19, from Delage; 20, 21, from Schütt.

(Fig. 10, *10-13*), the most Alga-like form, colonies of considerable size are formed by repeated division within a thick stratified gelatinous investment.

The Noctilucaceæ (Cystoflagellata) are probably derived from *Pyrocystis*-like Peridiniales. In *Noctiluca* (Fig. 10, *14*) the spherical cell shows great resemblance in internal structure to *Pyrocystis*, though there is no cell-wall and there are, on the other hand, some elaborations not found in *Pyrocystis*—e.g., the thick tentacle which is transversely striated and shows movements, the short flagellum in the gullet-like opening guarded by two projections ("tooth" and "lip"). The reproduction of *Noctiluca* is a somewhat remarkable process—after conjugation of two cells budding occurs, and from the buds there arise motile cells which show *Gymnodinium*-like features—a transverse groove (without flagellum, however) and on the concave ventral side a backwardly directed longitudinal flagellum. The other genera of the family—*Leptodiscus* (Fig. 10, *15*, *16*) and *Craspedotella* (Kofoid, 71)—also show specialised structure, and do not serve to fill the gap between *Noctiluca* and *Pyrocystis*; in *Leptodiscus* the cell has the form of a watch-glass, the convex ventral surface having a wide gullet-like depression on one side, and on the other and a narrow pit containing a flagellum, while *Craspedotella* resembles a medusa in form.

Reference has already been made to a possible connection between Gymnodiniaceæ and the Infusoria. Certain organisms are also known which appear to lead from the Peridiniales to another group of Protozoa—the Radiolaria. The flagellated spores produced by various Radiolaria (for details and some of Brandt's figures of these, see Gamble's account of this group in Lankester's *Treatise on Zoology*, 151) present an extraordinarily close resemblance to *Gymnodinium* and other simple Peridiniales, and suggest the origin of this Protozoan group from *Gymnodinium*-like ancestors. Moreover, Schütt has described three genera which appear to form direct links between Gymnodiniaceæ and simple Radiolaria, and which also suggest the possible origin of the Diatoms; these genera (*Gymnaster*, *Monaster*, *Amphitolus*) have an internal skeleton which recalls that of Radiolaria, and the body is divided into two portions by an equatorial suture, which in *Amphitolus* (Fig. 10, *21*) and *Monaster* (Fig. 10, *20*) is grooved, while in *Monaster* the resemblance to Peridiniales is enhanced by the presence of two flagella inserted in this groove and springing laterally from the body. In addition, Borgert has shown that certain genera—*Distephanus* (Fig. 10, *17-19*), *Mesoscena*, *Dyctiocha*, *Cannopilus*—which had been previously placed in the Radiolaria (in the bodies of which they live as commensals, and with which they agree in having a siliceous skeleton) are Flagellate forms, for which he formed the group Silicoflagellata (see also Lemmermann, 80, 83); these organisms have a skeleton consisting of transverse rings which are either free or joined up by longitudinal spicules to form a network, and in the genera named there is a single flagellum (Borgert's new genus *Ebria* has two flagella), while the protoplasm contains numerous yellow chromatophores. The Silicoflagellata may have been derived from forms like *Monaster*, or they may have come from Chrysomonadinean ancestors—certain Chrysomonads show a tendency to the formation of flinty skeletons (e.g., *Mallomonas*, *Chrysosphærella*). The Coccosphærales (Coccolithophoridæ, 83, 86, 87) are perhaps derived from simple Chromulinales; in general morphology they resemble forms like *Chrysococcus*, but with a peculiar armour consisting of calcareous plates instead of a homogeneous perisarc and suggesting comparison with the tesselated siliceous armour of *Mallomonas*, though until their cytology has been elucidated their affinities must remain in doubt.

In connexion with the Cryptomonads, mention may be made of two remarkable and somewhat aberrant Flagellate genera recently discovered by Scherffel,[1] the position of which in the scheme of classification above outlined appears to be doubtful. In one of these forms, *Monomastix*, there are two large laterally placed green chromatophores, each with a pyrenoid, and starch is formed; the cell shows dorsiventral symmetry and there is a single terminal flagellum. The other genus, *Pleuromastix*, is also a dorsiventral form, but has brown chromatophores and produces oil and probably also leucosin; it too has a single flagellum, inserted laterally at the obliquely truncate anterior end of the body. Scherffel inclines to the view that *Monomastix* belongs to the Polyblepharidaceæ, but Pascher (in reviewing Scherffel's paper in *Zeitschr. f. Bot.*, Bd. 5, 1913, p. 405) considers that its affinities lie rather with the Cryptomonads; both writers refer *Pleuromastix*, somewhat doubtfully, to the Chrysomonads. The most remarkable character common to these genera, apart from the possession of a single flagellum (all hitherto described Cryptomonads and Chloromonads have two flagella, though one order of Chrysomonads, the Chromulinales, is characterised by a single flagellum) is the presence of peculiar structures somewhat resembling the trichocysts found in some Chloromonads (*Rhaphidomonas*, *Merotricha*) and Peridiniales (*Polykrikos*, see above) as well as in the Ciliate Infusoria. These trichocyst-like organs, especially well developed in the green form *Monomastix*, consist of a highly refractive outer layer and a less refractive central mass which on treatment with various reagents is protruded rapidly as a filament (in *Pleuromastix* usually as a distinctly tubular structure). According to Scherffel, the structure of these organs in the two new Flagellates confirms the suggestion put forward by Künstler that the peculiar granular organs found lining the gullet-like depression in the Cryptomonad body represent rudimentary trichocysts. Among the Ciliate Infusoria corresponding organs occur, in addition to more highly organised trichocysts, and it appears probable that in both cases structures of this kind are not always to be regarded as defensive organs but may be merely products of secretion. Apart from its possession of pyrenoids and starch, *Monomastix* might well be placed in the Chloromonads, but on the whole it would appear that both genera may be perhaps best classed provisionally among the Cryptomonads—as here treated, this is a somewhat varied and generalised one, with many divergent affinities.

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[1] "Zwei neue trichocystenartige Bildungen führende Flagellaten." Arch. f. Protistenk., Bd. 27, 1912, pp. 94-128.

(*To be continued*).

NOTES ON RECENT LITERATURE.

AN EXTINCT ANTARCTIC FLORA.

In 1904 Prof. Nathorst[1] published a preliminary note on a collection of Jurassic plants obtained by Dr. J. G. Andersson in lat. 63° 15′ S., long. 57° W., in the course of a visit to Graham Land by Nordenskjöld's Swedish Antarctic Expedition (1901–3). Attention was drawn to the close resemblance of the plants as a whole to the Middle Jurassic Flora of East Yorkshire. A detailed description of the Graham Land plants has now been published by Dr. T. G. Halle[2], to whom Prof. Nathorst entrusted the work of interpreting these exceptionally interesting palæobotanical records. Prior to Anderson's discovery of the Jurassic flora, Capt. Larsen had collected some pieces of petrified wood on Seymour Island (lat. 64° 20′ S.), and from this locality the Swedish expedition obtained several Tertiary plants and a single coniferous twig of Cretaceous age resembling *Sequoia fastigiata* (Sternb.). The Tertiary plants were described by Dusén in 1908[3], and an account of the coniferous woods has been published by Dr. Gothan[4]. Members of Sir Ernest Shackleton's expedition found some fossil wood and recorded the occurrence of a seam of coal in lat. 85° S. The Graham Land plants were collected at Hope Bay in a dark slaty rock, capped by volcanic tuffs, which also afforded a few imperfectly preserved bivalves believed to be freshwater species.

Dr. Halle prefaces the descriptive part of his paper by some interesting remarks on the principles of classification or nomenclature of fossil plants, and states that he has "acted on the conviction that it is a lesser evil to keep forms separated which are identical than to identify such as are distinct." It is, on the other hand, arguable that as it is a sound general principle "to keep the mind open when there is no sufficient warrant for closing it"; so in the case of fossils, if there are no satisfactory reasons for separating forms which bear a close resemblance to one another, it is wiser to use specific names in a liberal sense. The real difficulty is that in dealing with more or less fragmentary remains of vegetative organs we lack adequate data on which to base conclusions as to the range of specific variation, and whatever guiding principle is adopted the student cannot as a rule achieve more than a provisional result. In one of his letters Darwin describes, in terms which will appeal to all who have attempted to determine impressions of fossil plants, the state of mind induced by his systematic work on Cirripedes—"After describing a set of forms as distinct species, tearing up my MS. and making them one species, tearing that up and making them separate, and then making them one again, I have gnashed my teeth, cursed species, and asked what sin I had committed to be so punished."

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[1] Compt. Rend., June 6th, 1904.

[2] "The Mesozoic Flora of Graham Island." Wiss. Ergebnisse der Schwedischen Südpolar-Expedition, 1901-1903. Bd. III, Lief. 14, Stockholm, 1913.

[3] "Ueber die Tertiäre Flora der Seymour-Insel." Ibid., Bd. III, Lief. 3, 1908.

[4] "Die fossiler Hölzer von der Seymour-Insel." Ibid., Bd. III, Lief. 8, 1908.

Halle writes in defence of his position—"Only, if the species are narrowly delimited, the eventually established relation between the floras will be much more reliable than if the opposite principle is adopted." This statement implies that the slight differences on which specific separation is based are something more than the expression of the plant's plasticity, and hardly takes sufficient account of the lessons taught by the vegetative organs of recent plants.

But these are questions of secondary importance, and in all systematic accounts of fossil floras the personal bias of the author must be the determining factor.

Dr. Halle's work is characterised by thoroughness and accuracy, and whether or not one may agree with all his determinations, his descriptions and illustrations are a substantial contribution of considerable value. The Equisetales are represented by a single species hardly distinguishable from the Indian Jurassic type *Equisetites rajmahalensis* Schimp. but referred by Halle to *E. approximatus*, a designation previously suggested by Nathorst. The widely spread Jurassic species *Sagenopteris Phillipsi* (Brongn.), for which Halle adopts the unfamiliar but older name *S. paucifolia* (Phill.), is represented by some well-preserved leaflets. Ferns are abundant, though unfortunately nearly all the specimens are sterile. The characteristic Middle Jurassic type *Todites Williamsoni* (Brongn.) occurs in both a sterile and fertile state, and some fertile pinnæ are described under the name *Coniopteris* cf. *nephrocarpa* (Bunb.), though the Yorkshire specimens on which Bunbury founded his species *Sphenopteris nephrocarpa* are usually regarded as indistinguishable from the protean type *Coniopteris hymenophylloides* (Brongn.), also recorded from Graham Land. The genera *Cladophlebis* and *Sphenopteris* appear under various forms; several new specific names are instituted, and in some cases on evidence which is hardly convincing. *Dictyophyllum* and sterile pinnæ probably, as Halle believes, identical with *Klukia exilis* (Phill.) afford other familiar instances of cosmopolitan Jurassic plants. Saporta's genus *Scleropteris* is revived for specimens similar to the European species *S. Pomelii* Sap. *S. furcata* Halle is described as characterised by the forking of the rachis, a feature which suggests comparison with Zigno's Italian species of *Dichopteris*, a genus omitted by Halle in his discussion of the characters of *Scleropteris* and *Pachypteris* though there would seem to be no adequate reason for discarding *Dichopteris* in favour of *Scleropteris*[1]. The difficulty of drawing a line between *Pachypteris* and *Thinnfeldia* is considered, and under the former name is included *P. dalmatica* Kern., a form to some extent transitional between *Thinnfeldia* and *Dichopteris*, which might reasonably be included in the latter genus.

Cycadean fronds form a conspicuous feature in the Hope Bay flora, including examples assigned to *Nilssonia*, *Pseudoctenis*, *Zamites*, *Otozamites*, *Ptilophyllum*, and a small specimen which may, as Halle suggests, belong to a *Williamsonia*. The generic name

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[1] Seward, "Fossil Plants," Vol. II, p. 552.

Zamites is used for several forms which agree much more closely with *Ptilophyllum* fronds than with *Zamites* as usually employed. Conifers are represented almost entirely by vegetative shoots, but the presence of Araucarian cone-scales of the *Eutacta* type is a feature of special interest; the seed-bearing scales are referred to Feistmantel's Indian species *Araucarites cutchensis*, but, as Halle points out, they also agree very closely with the English Jurassic species *A. Brodiei* Carr., not to mention other examples from South Africa, Scotland, and North America. Halle institutes a new genus *Elatocladus* for "sterile Coniferous branches of the radial or dorsiventral type, which do not show any characters that permit them to be included in one of the genera instituted for more peculiar forms." It is unfortunate that most of the generic names applied to fossil Coniferous shoots are based to a large extent on the cones, and these are frequently not preserved or occur apart from the vegetative branches. The nomenclature certainly needs revision. An objection to Halle's generic term as he defines it, and one which is recognised by him as a possible drawback to its extended application, is that it includes forms with leaves of the *Taxites* type as well as branches with leaves like those of *Sphenolepidium*, *Elatides*, and other genera. An alternative plan is to retain *Taxites* in the wide sense in which it is used by most authors for twigs bearing linear and usually distichous leaves similar to those of *Taxus*, certain species of *Podocarpus*, *Sequoia sempervirens*, and other recent Conifers, and to adopt the name *Pagiophyllum*, for forms with radially disposed leaves like those of *Elatides*, *Sphenolepidium*, and *Cheirolepis*. A species of *Elatocladus* instituted by Halle (*E. heterophylla*) affords an interesting example of dimorphic foliage which might well be compared with shoots of some recent species of the southern hemisphere genera *Dacrydium* and *Podocarpus*.

There can be no doubt that, as Halle says, the Graham Land plants are relics of a Jurassic flora, though some of them are identified, and no doubt correctly identified, with Wealden species. Although there are some common Jurassic types which have not as yet been recorded from this Antarctic region, notably *Ginkgo*, *Baiera*, *Phœnicopsis*, *Czekanowskia*, and others, the occurrence of several ferns and gymnosperms specifically identical with Arctic, North European, North American, and Asiatic Jurassic plants is a remarkable testimony to the world-wide distribution of a Mesozoic flora. The phytogeographical and climatological problems emphasized by this most recent contribution to Mesozoic Botany have not received the attention they deserve, and for this as for other reasons Dr. Halle's critical work is especially welcome.

The correlation of the Graham Land flora with that of East Yorkshire or with some of the Upper Gondwana floras of India cannot be regarded as necessarily carrying with it the implication that species common to Arctic, Antarctic, and other regions were in existence at the same time. As Huxley wrote, "There seems, then, no escape from the admission that neither physical geography nor palæontology possesses any method by which the absolute synchronism of two strata can be demonstrated."

A. C SEWARD.

LABORATORY NOTES.

SOME SIMPLE PHYSIOLOGICAL DEMONSTRATIONS.

BY

F. E. Fritsch, D.Sc., Ph.D.,

Professor of Botany, East London College, University of London;

AND

E. J. Salisbury, B.Sc.,

Lecturer in Botany, East London College, University of London.

[With One Figure in the Text].

In connection with a course of lectures recently given by one of us, a number of simple methods of physiological demonstration have been worked out, some of which seem to us to be of sufficient interest to warrant a brief description.

1. *An artificial stoma.*—Diverse models of stomata constructed of unequally thickened rubber are described by various authorities, but none of these are easily made, the materials are somewhat costly, and moreover, the results are not always satisfactory. The artificial stoma about to be described, though open to certain objections, has the great advantage over rubber-models that it can be made at any time and in the space of a few minutes. To construct such a model the stem of an herbaceous plant provides all the material that is required. We have found the scape of a jonquil, Narcissus or daffodil, and particularly the internode of the dog's mercury (*Mercurialis perennis*) to be perfectly satisfactory; the petiole of the cuckoo-pint (*Arum maculatum*) and the internode of the dead-nettle also furnish suitable material. A straight piece about three to four inches long (in the case of the dead-nettle one to two inches long) is selected and is halved lengthwise. The two halves thus obtained are then placed in strong salt solution until they become flaccid. They are thereupon placed parallel to one another in such a way that the original outer surfaces of the internode or scape are in juxtaposition, while what was previously the inner surface faces outwards. In this position the two halves are firmly tied together by string at their two ends (Fig. 1, B, *a*). If the two pieces thus joined together are placed in tap water, in the space of a few minutes they will (as they gain in turgescence) arch apart so as to leave a wide aperture between them (cf. Fig. 1, B, *b*)—in other words the pore of the artificial stoma opens. A return to the salt solution again results in the closure of the pore, and this sequence of events can be repeated several times. If the artificial stoma with the pore widely open is allowed to dry slowly by exposure to the air, a marked decrease in the width of the opening becomes manifest after some time, although the closure is not so complete as when due to plasmolysis.

The advantages of this model lie in the fact that it demonstrates the influence of changes of turgescence in leading to the opening and closing of the pore, and that the inner faces of our model guard cells consist of thicker material than the outer. On the other hand we are of course dealing with cell-complexes in place of cell-units, but as the method is intended only to demonstrate to a class the mode of action of the stomatal mechanism, this does not seem to us to be a vital objection.

2. *Continuity of the aërating system of the plant.*—The ordinary wash-bottle method[1] of illustrating this important fact depends entirely on obtaining a suitable leaf, and has the further drawback that it is not readily demonstrated to a class. By utilising an air-pump the continuity of air-spaces in the plant is of course readily shown, but the method about to be described only involves the use of materials that are to be found in any laboratory, and moreover, operates for some considerable length of time without attention. For the purpose of this experiment we use a round-bottomed flask, provided with a rubber cork, through a single hole in which a piece of glass tubing twice bent at right angles is inserted (Fig. 1, A). The one arm of the glass tube projects only for a short distance below the cork, while the other (free) arm is considerably longer. To the open end of the latter a branch bearing leaves or a single leaf is fitted by rubber tubing so as to make an air-tight connection, the cut end of the stem or petiole extending into the tube above the level of the surrounding rubber (cf. Fig. 1, A, *a*). Prior to doing this the long arm of the glass tube is partially filled with a column of water extending some four to six inches above the cut end of the stem or petiole (Fig. 1, A, *b*). The rubber cork with attached tubing is now taken out of the flask, and the latter is then half filled with water, which is heated until it has boiled for a minute or two. While the flask is still filled with water-vapour the rubber stopper is fitted into it, and the flask is placed in a vessel of cold water. The reduced pressure within the flask resulting from the condensation of the contained water-vapour leads to a strong suction, and as a result a stream of air-bubbles commences to arise from the cut end of the stem or petiole and to ascend through the column of water in the longer arm of the glass tube (cf. Fig. 1, A). This goes on for several hours, whilst the flask slowly cools. The stream of bubbles is so pronounced that the experiment is readily visible to a class of moderate size, whilst the result of the experiment, for demonstration to larger numbers, can easily be projected on to a screen by the aid of a lantern.

3. *Recovery of a flaccid shoot.*—The same apparatus can also be used to demonstrate the recovery of a flaccid shoot on being injected with water. For this purpose the upper end of the shoot is removed and the cut surface thus produced is attached as before to the long arm of the tube, whilst the lower end of the shoot is placed in a beaker of water. In order to prevent the entry of air into the tissues by way of the stomata both surfaces of the flaccid leaves should be vaselined. As a consequence the suction generated within the flask (as in the previous experiment) operates in causing a rapid flow of water through the shoot. After a little time the leaves become turgid.

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[1] Detmer and Moor. "Practical Plant Physiology" (1909), p. 172, Fig. 61.

4. *Rate of flow of water through the wood.*—For the purpose of this experiment, as for others ordinarily requiring the use of an air-pump, the same method as described in the two previous cases can be employed. By a simple modification it can be adapted for comparative results. Thus, if the flask in Fig. 1, A, be fitted with a two-holed stopper, *each* hole bearing a piece of glass tubing like that shown in the figure, the rate of flow through two branches (*e.g.*, those of a Dicotyledon and a Conifer), subjected to identical amounts of negative pressure, can be compared. The upper cut

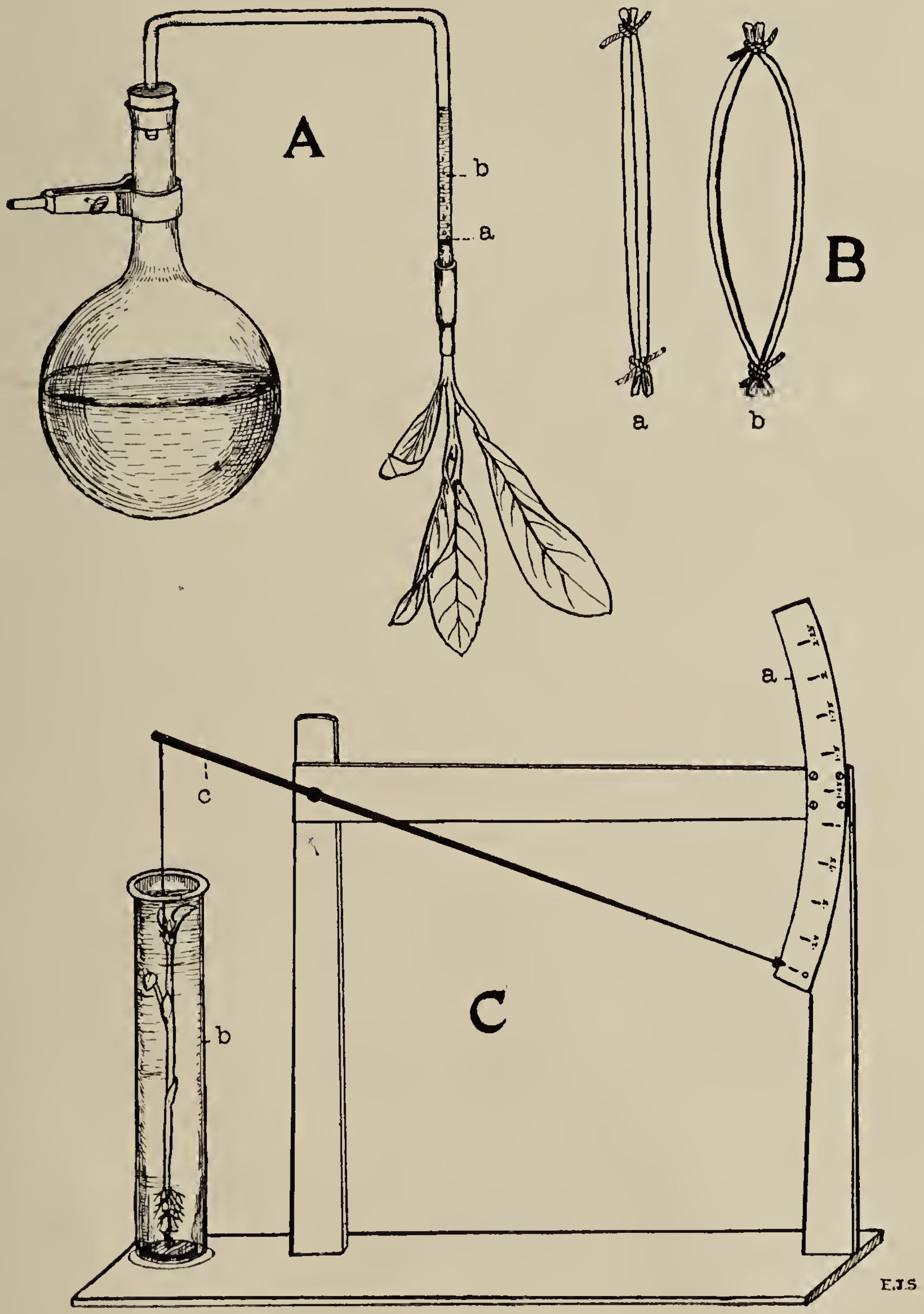

Fig. 1. For description see Text.

ends of the branches are fitted on to the free ends of the glass tubes with rubber tubing as before but without the column of water above, while their lower ends dip into beakers filled with water. The surface of the branches should previously be coated with a layer of paraffin wax so as to close up all apertures and scars. The relative conducting powers of the two branches will of course be proportional to the heights of the columns of water that form in the glass tubes above their cut ends.

5. *Demonstration of water-pores.*—We have adopted the same principle for the rapid demonstration of water-pores. To the longer arm of the tube is attached a glass cylinder supplied at both ends with rubber corks perforated by a single hole and sufficiently wide to accommodate the leafy portion of the branch to be experimented with. The branch is inserted through the hole[1] in the lower cork so that its foliage is situated within the glass cylinder, whilst the lower cut end of the branch projects below the cork into a beaker of water. Owing to the reduced pressure produced in the apparatus as before, a considerable quantity of water is sucked up into the shoot, and drops of moisture are soon formed over the water-pores. Branches of *Fuchsia* give a good result.

6. *Demonstration of the shrinkage of an herbaceous plant as the result of loss of turgescence.*—The importance of turgescence in maintaining the rigidity of an herbaceous plant is easily demonstrated by familiar methods, but a means of making the resulting shrinkage obvious to a whole class has not, as far as we are aware, been yet described. We use for this purpose a simple lever working over the surface of an arc, graduated to show the actual distance to which the movement of the long arm of the lever corresponds (Fig. 1, C). To the short arm of the lever (*c* in Fig. 1, C) an entire herbaceous plant is firmly tied by its apex, and to the other end of the plant is attached a weight sufficiently heavy (one to two pounds) to keep the plant in position at the base of the glass cylinder *b* (Fig. 1, C). The latter should be tall enough to include the whole plant. If necessary, sufficient weights can be attached to the long arm of the lever to keep the plant fully extended without undue strain. The cylinder is now carefully filled with strong salt solution and the position of the pointer on the graduated arc noted. After about half-an-hour the pointer on the arc will record a shrinkage of a quarter to half an inch according to the nature and size of the plant used in the experiment. If the salt solution is then siphoned off and replaced by water, the gradual recovery of the plant can be noted in the same way.

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[1] An excellent method of fitting a branch into a rubber cork is described and figured by Osterhout, "Experiments with Plants," 1908, p. 205, Fig. 118.

REVIEW.

ALPINE AND SUBALPINE PLANTS.

Alpine Plants of Europe, together with Cultural Hints. By Harold Stuart Thompson, F.L.S. Pp. xvi + 274 + 64 coloured plates and a General Map of the Alps. London: George Routledge & Sons, Ltd., 1911. Price 7*s*. 6*d*.

Subalpine Plants, or Flowers of the Swiss Woods and Meadows. By H. Stuart Thompson, F.L.S. Pp. xvi + 325 + 33 coloured plates and a (contoured) Map of the Alps (Bartholomew). London: George Routledge & Sons, Ltd., 1912. Price 7*s*. 6*d*.

MR. STUART THOMPSON'S two books are designed to supply the need of well illustrated English works describing the more beautiful and interesting species indigenous to the High Alps and the subalpine region (i.e., from about 3,000 to 5,000 feet) respectively. It has been remarked that while the plants of the High Alps (the alpines proper) are, on account of their beauty and their striking difference from those of the plains, naturally those which attract the greatest notice from visitors to Switzerland, nevertheless most of the mountain resorts are situated in or but slightly above the subalpine zone, and the tourist interested in Botany therefore needs something more than descriptions of the "high alpines" alone. From this point of view the two books before us most usefully supplement one another. At the same time, each is complete in itself, for of course no rigid line has or can be drawn between the two floras: many of the subalpines range up to great altitudes and some of the high alpines descend well into the subalpine zone.

The plan of both books is the same. The bulk of the work consists of systematic descriptions of a large selection of the indigenous plants, illustrated by coloured plates on each of which several species are grouped, and prefaced by a few chapters dealing with the nature, characteristics, and distribution of alpine and subalpine plants, with their culture in "rock-gardens," with the best methods of collecting and preserving them, and so on. The second book has also an interesting chapter on the gardens which have been established, especially during recent years, in various parts of the Alps.

In the introductory chapters Mr. Thompson discusses the question of altitude in relation to the distribution of plants, and points out that so many factors are involved as to make it impossible in the vast majority of cases to lay down anything like exact altitudinal limits for the distribution of a species. Climate, exposure (really involving a local change of climate), soil, and physiography all profoundly influence the heights at which different species grow. At the same time many useful altitudinal data, largely based on Mr. Thompson's own observations, are recorded in these books. The second work (*Subalpine Plants*) also contains a useful comparison with the Flora of Britain.

The descriptions are clear and concise and not overburdened with technical terms: a glossary is added for the use of the non-botanical reader. The importance of full descriptions of the habitats and distribution of the different species is very great, and has been fully recognised by the author. The species which occur in Britain are so noted, but not in quite all cases. It would have added considerably to ease of reference and the value of the comparison if the allusion to Britain had been given uniformly throughout with the addition of the distribution of the species within the British Isles where this is of interest: e.g., *Epilobium angustifolium*, British (general); *Sedum album*, British? (rare, perhaps alien); *Saxifraga tridactylites*, British (general); *S. stellaris*, British (mountain); and so on. It is not clear why the nativity of the Yew in the British Isles should be doubted.

The coloured plates in *Alpine Plants of Europe* are taken from Seboth's book, which was translated into English by the late A. W. Bennett some years ago, and of which the copyright has, we understand, passed into Messrs. Routledge's hands. They are of varying merit, but on the whole good. *Subalpine Plants* is illustrated by Mr. Flemwell, some of whose drawings are of remarkable truth and beauty. The sprays of different plants, three or four or more of which are represented on each plate, are, however, sometimes rather irritatingly mixed up, and a wide space is wasted in margin, so that the reduction of the drawings (to 4-7ths natural size) is unnecessarily great, and in the case of the smaller plants a serious defect.

Mr. Thompson's books are primarily intended, no doubt, for the tourist who knows something of field-botany and classification: the pure novice would find it difficult to use a systematically arranged book, and to such a one Schröter's *Taschenflora des Alpenwanderers* may be recommended for the first week or fortnight, at least. On the other hand, the serious student naturally buys the best available flora of the country or region he visits, in which he may be sure of finding the most complete information and the results of the latest work. But for the large class of readers who come between these two, Mr. Thompson's books may be cordially recommended. Nor will they be without use for the advanced student, owing to the inclusion of Pyrenean and other high mountain plants, and to the wide personal knowledge of species in the field which the author possesses—perhaps, as regards western Europe, to a greater degree than any other English botanist.

We are glad to hear that Mr. Thompson is preparing a somewhat similar work on the Plants of the Riviera, which will bear the same relation to Penzig's excellent little *Flora de poche du Littoral Mediterranêen* as the books under review bear to Schröter's *Taschenflora des Alpenwanderers.*

A.G.T.

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PHENOMENA AND PROBLEMS OF SELF-STERILITY.

BY R. H. COMPTON.

UNTIL recently, perhaps no branch of Plant Physiology and Biology was in so obviously backward a state as the study of Self-Sterility. While our ignorance of the processes and causes of this group of phenomena is still profound, new lines of research have been laid open during the last few years, and there is every prospect of rapid accessions to our knowledge in the immediate future.

I.—THE INCIDENCE OF SELF-STERILITY.

The facts as to the incidence of self-sterility are complex and baffling. It is probable that in many cases records of self-sterility rest on faulty observation. Some plants have been named as self-sterile in the absence of all evidence that pollen ever reached the stigma! Other less glaring errors have arisen through the absence of the necessary conditions for the germination of pollen: for instance, *Laburnum vulgare* was long regarded as a typically self-sterile plant, for although the stigma is surrounded with pollen no seed is set in the absence of insects. Jost (1907), however, found that in this case pollen will fertilise the ovules of the same flower if the stigma be slightly injured by rubbing or pricking—such injury being produced in nature by insect visits.

Such cases are clearly of the nature of mechanical hindrances to fertilization, and have nothing to do with self-sterility proper. In *Corydalis cava* also, pollen-tubes will not enter the stigma unless the latter be injured; but in this case there is the additional phenomenon of true self-sterility. In the case of pollen from the same flower the tubes only penetrate a very short distance into the injured stigma, and fail to cause fertilisation: but foreign pollen is able to produce tubes which grow down to the embryo-sac and bring about fertilisation (Jost 1907).

Of two species of the same genus one may be self-fertile the other self-sterile, as in the case of *Corydalis lutea* and *C. cava* respectively. *Lilium bulbiferum* is self-sterile, but the sub-species *L. Buchenavii* is self-fertile (Jost 1907). Kirchner (1905) has shown that on the whole the perennial members of the Leguminosæ are self-sterile, the hapaxanthic self-fertile. Certain cultivated varieties of Plum (*Prunus domestica*) and Cherry (*P. cerasus*) are highly self-sterile (with slight parthenocarpy, *i.e.*, growth of the fruit though not of the seed), others self-fertile (Backhouse, 1911). Some individuals or races of a species may be highly self-sterile; others, taxonomically indistinguishable, self-fertile. This is the case, for instance in *Reseda odorata* (Darwin, 1876): and apparently also in the Tunicate *Ciona intestinalis*, which Castle and Morgan (1905, 1910) find to be self-sterile in America, but which Potts (1910) finds self-fertile at Naples. On the other hand a change in environment may produce a marked effect: as in the cases of *Eschscholtzia californica* and *Abutilon darwinii*, self-sterile in their native Brazil but moderately self-fertile in England (Darwin, 1876). *Passiflora alata* is said to have been rendered self-fertile by being grafted on a distinct species. *Biophytum sensitivum* is said to be self-sterile in its open, self-fertile in its cleistogamous flowers. It is probable that, in some cases of partial self-sterility, geitonogamy produces more seeds than autogamy though less than xenogamy.

Further, the degree of self-sterility varies enormously. In a great many cases the offspring of a self-pollination are slightly fewer than those of a cross-pollination:[1] at the other extreme there are a few cases in which the stigma and pollen of the same flower are mutually poisonous.

Clearly there are very many problems awaiting solution with respect to the causation of self-sterility and the reasons for its apparently capricious incidence.

II.—CAUSATION OF SELF-STERILITY.

From the standpoints of Chemistry and Morphology there is the problem of the exact nature of the hindrance to self-fertilisation.

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[1] The offspring of a self-pollination are often not merely fewer but weaker than those produced by a cross. This is probably a different phenomenon from that of the evil (or good) effects arising from in-breeding, which it is customary to explain as due to the increased chance of the meeting of similar recessive characters in consanguineous matings. Nor is it a phenomenon of self-sterility in the strict sense, for fertilisation occurs: but it may be suggested that the incompatibility between paternal and maternal tissues which brings about the failure of a percentage of fertilisations may also apply as between the paternal and maternal portions of the protoplasm in each cell of the zygote, and that weakliness of constitution is the result.

Morgan has carried out a series of experiments on *Ciona intestinalis* with the object of locating the seat of the phenomenon and assigning a proximate explanation. He concludes that "immunity of the egg to its own sperm is due to the failure of the sperm to call forth in the egg of the same individual the reaction that leads to the absorption of the spermatozoon. The failure to self-fertilise is a specific reaction that takes place or fails to take place at the surface of the egg itself" (1910, p. 233.)

In the higher plants, owing to the complexity of the mechanism of siphonogamy and angiospermy there are a great number of theoretically possible causes of self-sterility. The most extensive study that has been made of the subject is that of Jost (1907). The result of his experiments is to show that the cause of the failure to fertilise in the case of self-sterile plants (*Corydalis cava*, *Secale cereale*, *Lilium bulbiferum*) is concerned with the passage of the pollen-tube through the style. Since the growth of the pollen-tubes is entirely inter-cellular, it follows that the chemical substance responsible for furthering the growth (whether by means of nutrition or of stimulation) or for hindering it, must be soluble and diffusible: but no artificial culture medium was discovered in which pollen-tubes could grow to nearly the extent necessary to produce fertilisation.

Pollen-grains, like fungus spores, can germinate on many culture media, and, as Strasburger has shown (1886), on the stigmas of a great variety of plants of distinct species. But the full growth necessary for fertilisation can only result under a very limited set of conditions.

It may be remarked that the feeble growth of pollen-tubes in the stigma in cases of self-pollination may have the same cause as their failure in artificial culture: and that this may be similar to that which Morgan found in *Ciona*, viz., the failure to evoke the necessary reaction from the tissues of the style. This may indicate that the soluble diffusible substance in question acts in a positive manner, by furthering the growth of pollen-tubes in xenogamy.

III.—Analogy with Immunity.

On the other hand, the analogy with the phenomena of immunity to which Jost calls attention, leads to the opposite conclusion. we compare pollination with fungal or bacterial infection it might be expected that the result would be the formation of anti-bodies. The work of Schiff-Giorgioni (1905) on *Bacillus oleæ*, and of Bernard (1909) on the Fungi which inhabit the roots and tubers of Orchids, has proved the existence in plants of antitoxin reactions quite parallel with those observed in animals. The visible effects of the development of the pollen-tube within the style, namely the enlargement of the ovary, the withering of the stigmas, etc., are strikingly suggestive of the phenomena of gall-formation (often so specific and stereotyped), hypertrophy and degeneration under the attacks of a fungal parasite. Both in gall-formation and in fertilisation the chemical nature of the stimuli and reactions has so far eluded investigation.

If there be an analogy between fertilisation and infection, there is also one between sterility and immunity. There seem to be two main methods by which immunity is attained. In one the host is constitutionally resistant to the attacks of the parasite, this being the more frequent method. In the other the host is over-susceptible, and the attack of the parasite produces a quantity of decomposing matter which inhibits its further growth. Both these methods are paralleled in cases of failure of fertilisation. The first is the more usual: the pollen grains fail to germinate, or they germinate but the tubes do not flourish. The second occurs in certain cases of pollination from a distinct species, as recorded originally by Gärtner (1849), where the pollen appears to act injuriously on the stigmas: and also in the remarkable cases of self-sterility in certain Orchids mentioned above, where the same phenomenon occurs.[1]

The immunity of certain races of Wheat to the rust disease apparently belongs to the second category: *i.e.*, it is the result of over-susceptibility. The first attack of the fungus hypha causes so much decomposition of the tissues of the host in its immediate neighbourhood that its extension into the adjacent tissues is checked (Marryat, 1907): much in the same way that the wall of an abscess prevents the bacterial growth spreading far from the original seat of infection. The work of Biffen (1907) has shown that susceptibility to rust in Wheat behaves as a Mendelian dominant to immunity. Therefore, on the presence and absence theory, susceptibility is due to the presence of some substance which immune individuals lack. This substance thus seems to act as a partial check to the too energetic onslaught of the parasite in the susceptible plant. It might be expected that the same would obtain in the cases of self-sterility through decomposition; but here evidence is lacking.

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[1] In one case, that of *Oncidium flexuosum*, self-pollination and pollination from a species of *Notylia* both produced the same injurious effect (Darwin 1905 ii, p. 145).

IV.—INHERITANCE OF SELF-STERILITY.

Breeding experiments have however been performed in two cases of self-sterility; though in neither instance have the results so far been published in full. Baur (1911, p. 212) working with *Antirrhinum-majus* (self-fertile) and *A. molle* (self-sterile) finds that the F_1 hybrid is self-fertile, and that F_2 consists of a majority of self-fertile and a minority of self-sterile plants: exact countings not having been made. Compton (1913) has published a preliminary note on his experiments with *Reseda odorata*, a species in which certain individuals are self-fertile, others self-sterile. The work is incomplete, but seems to show that self-fertility behaves as a simple Mendelian dominant to self-sterility.[1] In these cases the simplest explanation appears to be that self-sterility is due to the absence of some substance either nutritive or stimulating to the growth of the pollen-tube. On the assumption that self-sterility is due to the formation of an anti-body, self-fertility would result from the presence of a substance which inhibits the action of the anti-body (as do the anti-immune-bodies and anti-complements of Ehrlich in the case of immunity).

Spermatozoa are known, from the experiments of Landsteiner, Metchnikoff and Moxter, to be able to call forth immunity against similar spermatozoa in the blood serum of an animal into which they are injected. Loeb considers that part of the effect of a spermatozoon in stimulating the development of an egg (namely the precipitation of the membrane) is due to the introduction of a lysin. It may be, therefore, that the acquired immunity of serum against spermatozoa is due to the development of antilysins. The individual and group differentiation in the hæmolytic anti-bodies produced by different animals of the same species, as demonstrated by Ehrlich and Morgenroth, may be paralleled in the similar differentiation in cases of self-sterility: and it is suggested that the two sets of phenomena may have the same kind of explanation in terms of the specific neutralising reactions of organisms to hetero- or auto-intoxication.

V.—SELF-STERILITY A RACIAL CHARACTER.

The problem of self-sterility as understood until recently involved a problem of individuality. It was believed that a self-sterile plant is fertile when pollinated from any other plant of the same species: it was thus necessary to assume that in respect of the mechanism of fertilisation every individual plant differed markedly—chemically or structurally—from every other. This assumption is almost unthinkable and numerous attempts have been made to show that it is in fact incorrect. Indications were not wanting that cross-pollination does not always give uniformly good results. For instance Müller (1873) found that in self-sterile species of *Abutilon* there is often more or less complete failure to set seed in crosses between closely related plants, *e.g.*, between parents and children, between sisters, and between half-sisters. Morgan (1905) too, as a result of extensive experiments on *Ciona intestinalis*, came to the conclusion that "it is not true that the sperm of a given individual will fertilise equally well the eggs of al other individuals."

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[1] Mention may also be made of the result obtained by East (1913), who found that on crossing *Nicotiana alata grandiflora* with *N. forgetiana*, both self-fertile species, the F_1 plants were completely self-sterile but fertile *inter se*. Further statements will be awaited with interest.

VI.—The Work of Correns.

Correns (1912) has recently made a partially successful attempt at solving the problem of the sterility of near kin *inter se*. He assumes that self-sterility is due to the presence of inhibitory substances (*Hemmungsstoffe*), but does not thereby wish to prejudge the question whether they are true inhibitors or whether they represent the lack of the means of furthering pollen germination and growth. The problem can therefore be stated as follows: Are these inhibitory substances individual (*Individualstoffe*) or are they racial and hereditary (*Linienstoffe*)? Correns reduced the experiment to its simplest form by taking two individuals (called **B** and **G**) of *Cardamine pratensis* of distinct origin, and crossing them reciprocally. The offspring (which may for our present purpose be considered together) were tested individually by pollinations (1) from the parents, (2) on the parents, and (3) from sisters. The results were far from simple, as the degree of fertility fluctuated widely, but Correns was able to draw from them the highly interesting conclusion that self-sterility depends on racial hereditary factors and is not a purely individual phenomenon.

The experiments in which the F_1 plants were pollinated from their parents **B** and **G** are the most instructive. It was found that these fell into four distinct classes according to their behaviour, as follows:—(1) Plants fertile with both **B** and **G**: these are regarded as lacking both the inhibitors which rendered **B** and **G** self-sterile, and may be written bg. (2) Plants sterile with both **B** and **G**, and therefore considered to have both of the inhibitors: these may be represented as BG. (3) Plants fertile with **B**, sterile with **G** (written bG). (4) Plants sterile with **B**, fertile with **G** (written Bg). It was found that these four classes were nearly equal numerically; the actual numbers were 16 bg, 16 bG, 14 Bg, 14 BG.

Let us now assume[1] that the genetic constitution of the plant **B** can be written *Bbgg*: the presence of the factor *B* renders the plant self-sterile (whatever characters its gametes may carry): similarly **G** would have the formula *bbGg*; *G* being another inhibitory factor distinct from *B* but alike causing self-sterility in the plants that carry it.[2] **B** produces gametes of two kinds, *bg* and *Bg*: **G** produces gametes *bg* and *bG*. The fertilisation of **B** by **G** or *vice versa* results in the production of four kinds of offspring in equal numbers; viz., *bbgg*, *bbGg*, *Bbgg* and *BbGg*: these are of the types bg, bG, Bg and BG respectively, as tested by crosses with **B** and **G**.

This Mendelian theory is on the whole consistent with the results of the other experiments, and it may be accepted as a crude account of the phenomena, although there are certain obvious objections to it in this simple form.

VII.—CRITICISMS OF CORRENS' THEORY.

The first criticism that can be made is to point out the numerous irregularities in reaction of one and the same plant to the same repeated pollination test, and the great difficulties of classification of the results. The second difficulty lies in the fact that the plants of the type bg are not self-fertile, though they lack both inhibitors: if it be assumed (as indeed is necessary for other reasons) that the self-sterility of the bg plants is due to their possession of a number of other inhibitors *H*, *J*, *K* . . . . , so that their true formula would be of the nature of *bbggHhJjKk* . . . . , this raises a new difficulty as follows. Let the formula of **B** be *BbggHh* and of **G** be *bbGghh*: then their offspring will be found in the following table:—

BgH *bGh* i	*Bgh* *bGh* ii	*bgH* *bGh* iii	*bgh* *bGh* iv
BgH *bgh* v	*Bgh* *bgh* vi	*bgH* *bgh* vii	*bgh* *bgh* viii

Of these eight classes of offspring Nos. i, ii, and iii will be sterile when pollinated from **B** and **G**; Nos. v, vi and vii will be sterile with B, fertile with G; No. iv will be fertile with B, sterile with G, and No. viii will be fertile with both B and G. The ratio of types would therefore be 3 BG : 3 Bg ; 1 bG : 1 bg, instead of equality. The discrepancy would be increased the greater the number of inhibitory factors acting: thus for four such factors the ratio of types would be 9 BG : 3 Bg : 3 bG : 1 bg.

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[1] The notation used here is that most in favour among students of heredity in this country, and differs slightly from that employed by Correns.

[2] Since plants containing the same inhibitory factor are sterile *inter se*, it is clear that homozygotes of the type *BB* and *GG* cannot occur.

These difficulties are recognised by Correns, who only advances the theory tentatively in the absence of full evidence.

VIII.—APPEARANCE OF SELF-FERTILE RACES.

One consequence of the theory may be pointed out. At every fertilisation there must arise individuals homozygous for the absence of one or more of the inhibitory substances. Therefore it is theoretically probable that occasionally an individual homozygous for the absence of *all* the factors would be produced. Such an individual would be self-fertile. It may be recalled that Darwin (1876) as a result of repeated self-pollinations of partially self-sterile plants through a series of generations obtained ultimately, in the cases of *Ipomœa purpurea* and *Mimulus luteus*, highly self-fertile plants. It is suggested that this phenomenon may be due to the weeding-out of the partial inhibitors through constant in-breeding, and that the self-fertile plants are the ultimate recessives. In some such way the self-fertile race of *Reseda odorata* may have arisen from the self-sterile.[1]

IX.—SELF-STERILITY AND SEX.

It is possible that the phenomena of self-sterility are more widely distributed than is generally realised. Indeed it may be said that they are intimately connected with sex differentiation. The current theories of sex for the most part leave unexplained the singular fact that male gametes do not fuse with male, nor female with female.[2] In the higher animals and plants the gametes and accessory sexual structures are highly specialised, and the inability of like to fuse with like is not so surprising at first sight. In the isogamous Algæ and Fungi, however, it is not by any means an expected phenomenon: it is not obvious why the gametes produced by one and the same individual of certain species of *Spirogyra*, or

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[1] The objection that in *Reseda* self-fertility is dominant is met by the reminder that the "inhibitory factor" may *ex hypothesi* be lack of nutrition or stimulus for the pollen-tubes:—a view of the matter favoured, as we have seen, by the chemical evidence and the analogy with immunity.

[2] Such a process takes place, however, in the parthenogenetic oogonia of *Humaria granulata*, where potential ♀ nuclei fuse in pairs: and something similar occurs in the fusion of polar nuclei in the Angiosperm embryo-sac.

Dasycladus clavæformis, or a heterothallic *Mucor* or *Phycomyces* should be unable to conjugate.

It may be suggested that this is in reality a simple case of self-sterility. In a plant like *Cardamine pratensis* self-sterility may depend, it seems, on one or more of several hereditary factors, and consequently there are a large number of distinct self-sterile races. The fewer the factors the fewer the races; with one factor only two kinds of individuals are possible, *viz.*, the heterozygote, and the homozygote for absence of the inhibitor: such a species would consist partly of individuals which could only be cross-fertilised, and partly of those which could both be self-fertilised and crossed; a condition possibly occurring in some species of *Spirogyra*, though here as in all other isogamous Algæ our knowledge is quite insufficient to make this suggestion either plausible or the reverse.[1] In the Mucorinæ the peculiar so-called sex-differentiation may quite conceivably be associated with true phenomena of self-sterility of a simple type: homothallic species would be those without inhibitory factors, heterothallic species would possess perhaps two such inhibitors.

It is clear that these suggestions break down at certain points, or require modification—just as do those of Correns on which they are founded. The chief conclusions that must be drawn are that our knowledge of the facts is insufficient to bear the weight of any but the most tentative hypotheses; and that the new view of self-sterility which we now possess as a result of Correns' work is likely to be of the greatest value in solving many of the most interesting problems in the whole range of Plant Biology.

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[1] Experiments are in progress which it is hoped may throw light on this problem.

BOTANY SCHOOL,
CAMBRIDGE.
April, 1913.

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ON A DISEASE OF GREENGAGE TREES CAUSED BY *DERMATELLA PRUNASTRI* PERS.

BY W. J. DOWSON.

[WITH THREE FIGURES IN THE TEXT].

I.—INTRODUCTION.

MY investigation of this disease was made at the suggestion of Mr. F. T. Brooks, who had for some years past noticed it to be present in the greengage plantations at Willingham and Cottenham near Cambridge. Little beyond the name and the distribution of this fungus was known and it was hoped that a thorough investigation of its life history in regard to its presence on greengages would be made. Unfortunately the work has been cut short owing to the fact of my leaving England; but as certain definite results have been obtained by investigation of the tissues of diseased branches and with pure cultures, it was thought worth while to record the work as far as it had gone.

Inoculation experiments were made, but of too recent a date to allow of any detailed examination at the time of writing. One or two, however, were investigated, and the results are here given.

I take this opportunity of expressing my sincere thanks to Mr. Brooks for his constant advice and criticism during the short time I have been able to devote to the work. My thanks are also due to Professor Seward who very kindly permitted me to carry on the investigation in the Botany School, Cambridge.

The fungus has been described under the following names:—*Peziza Prunastri* Pers., *Cenangium Prunastri* Fries, *Dermatea Prunastri* Fries, and *Tympanis Prunastri* Wallr. The conidial stage has been described as *Sphæronema spurium* (Fr.) Sacc. Saccardo refers to it as *Cenangium Prunastri*. Rabenhorst, referring to it as *Dermatella Prunastri*, considers the group genus *Dermatea* to be subdivided into three sub-genera of which *Dermatella* is the third, the others being *Eudermatea* and *Pezizicula*. Tubeuf and Engler and Prantl follow Rabenhorst's classification in which the group genus *Dermatea* is placed in the family *Cenangiaceæ* of the order *Pezizineæ*. Tubeuf in his "Pflanzenkrankheiten" mentions it as parasitic upon various varieties of plums; as does also Sorauer who in his "Handbuch der Pflanzenkrankheiten" (Bd. II, 1906), refers to it as *Dermatea prunastri.*

II.—CULTURE MEDIA.

Agar-agar was used throughout to stiffen decoctions of Victoria-plum wood, greengage wood, and grape juice. All three media were just slightly acid. Sterilised blocks (30 × 16 × 6 mm.) of greengage wood and sterilised pieces of bark of the same were also employed.

III.—FIELD OBSERVATIONS.

Among the greengage and victoria plum plantations which are to be found in the neighbourhood of Cambridge, the fructifications of *Dermatella prunastri* have been recently noticed upon some of the dead branches of both young and old trees. The greengages were chiefly attacked, but the *Dermatella* has also been found once upon a Gioborne plum. The diseased branches and twigs were evidently affected with some sort of "die back," and it was thought likely that the association of *Dermatella prunastri* with the "die back" condition was more than accidental. Several expeditions were made in the autumn of 1912 to Willingham where certain fruit plantations contain large numbers of greengage trees.

The dead branches were easily distinguished from healthy ones by the fact that they were covered with *Pleurococcus* sp. and lichens, whereas the healthy branches and shoots were fairly clean. Branches of various ages showed signs of attack, and ranged from twigs of a few years growth to old branches as thick as a man's wrist. Some portion of these dead branches bore the fructifications of *Dermatella*, and these were generally the distal parts which were covered fairly completely with the pycnidia and apothecia of the fungus (Fig. 1). Sometimes these were observed towards the proximal end of the branch, either in large groups or in smaller patches scattered irregularly over the whole branch. Occasionally the fructifications were seen on the bark of a trunk. The bases of some branches which were quite dead bore fructifications, but in others in which the basal part was apparently unaffected the fruit bodies were situated at some distance from the junction between the diseased and healthy tissues. I use the word "apparently" advisedly because the line of demarcation as seen in the cortex and older wood does not always coincide with the junction in the interior of a branch.

Many cases were found in which an oblique junction occurred as shown by the condition of the cortical tissues (Fig. 2); but upon cutting sections through such a branch below the outward line of demarcation it was found that the pith and first-formed rings of wood were also diseased. In fact a cylinder of diseased wood might be present which extended some considerable distance (1-2 feet) beyond the region of the infected cortical tissues. Cases with a fairly straight although oblique junction were also observed in which there was no central cylinder of diseased tissue which penetrated beyond the outer limit of discolouration. It was in these cases that most gumming was observed at the actual junction of healthy and diseased tissue, the latter being much discoloured particularly at the line of demarcation.

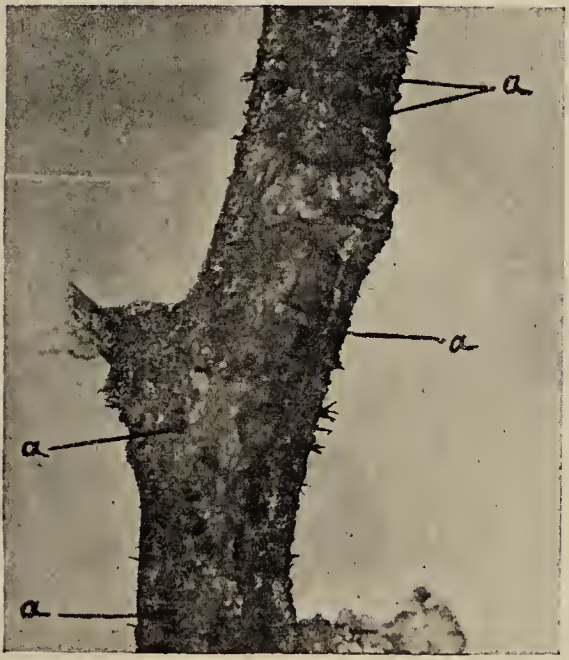

FIG. 1.

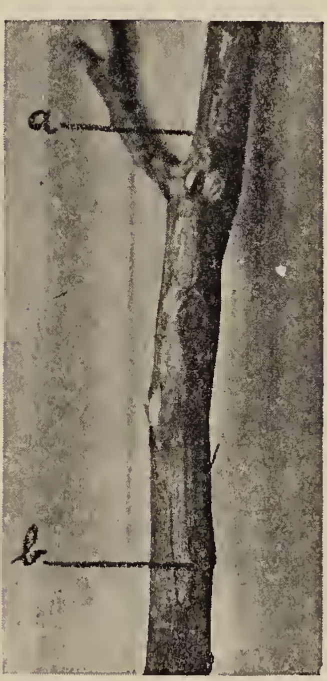

FIG. 2.

Fig. 1. *Dermatella prunastri* Pers. on greengage branches: *a*, apothecia; the needle-like projections are pycnidia. Nat. size.

Fig. 2. *Dermatella prunastri* Pers. on greengage branches: *a*, upper, and *b*, lower limit of an oblique junction area; the bark has been stripped off showing the discoloured wood above and to the right of the line *a b*. Two-thirds nat. size.

Upon examining more minutely a dead branch which bore fructifications, the button shaped apothecia were seen scattered sparsely among the very numerous pycnidia. Both fructifications were black in colour. Some clusters of pycnidia and apothecia arose together; both, however, occurred separately in twos and threes or singly.

IV.—DETAILED EXAMINATION OF *DERMATELLA PRUNASTRI* PERS.

The pycnidia, formerly thought to be a distinct fungus and called *Sphæronema spurium* (Fr.) Sacc., are elongated conical-shaped structures 1—2 mm. long which arise in the cortex a little way below the cork layer. They consist for the most part of a hard pseudo-parenchymatous tissue deeply pigmented on the exterior. From the basal portion ramify numerous hyphæ between the cortical cells. The upper distal part of the pycnidium is a narrow, short, hollow cylinder lined with the conidia-bearing hyphæ, whilst the lower part of this columnar structure is composed of sterile tissue. The conidia are produced in enormous quantities and are small ($20\mu \times 2{\cdot}5\mu$), crescent-shaped, unicellular hyaline spores, often with a highly refractive globule placed at the centre (Fig. 3, A). This body on staining proved to be the nucleus. In a damp atmosphere the conidia are extruded in coiled threads from the pycnidia, which were found to be numerous in autumn and throughout January.

The apothecia are small (·5—1·5 mm. in diam.), button-shaped bodies which are soft and slightly gelatinous in a damp atmosphere but hard and leathery when dry. The disc is provided with a narrow rim and is raised from the surface on a short thick stalk slightly embedded in the cortex. They are black in colour, and with the exception of the upper surface (hymenium) which is covered with asci and paraphyses, are composed of a pseudo-parenchymatous tissue. The asci are club-shaped (Fig. 3, B) and are surrounded by paraphyses which contain a dark coloured pigment in their upper portions which gives a blackish appearance to the hymenium. The paraphyses are branched and multi-septate (Fig. 3, B). The apothecia were not so numerous in January as in December.

The ascospores are variable in shape and size, and may be crescent-shaped, straight or oval, from 10—20μ long and 5μ broad. These spores are filled with small globules of fat or glycogen to such an extent that the septa are rarely seen in unstained preparations (Fig. 3, C). In preparations stained in Delafield's hæmatoxylin or in Heidenhain's iron-alum-hæmatoxylin, the septa are well seen and vary in number from one to four, the most usual number being two (Fig. 3, D).

V.—THE MYCELIUM IN THE WOOD.

Owing to the great amount of gum present in the diseased wood some difficulty was experienced in staining sections cut from such areas. The most useful stains proved to be Delafield's hæmatoxylin and the combination Methyl green and Congo red in watery

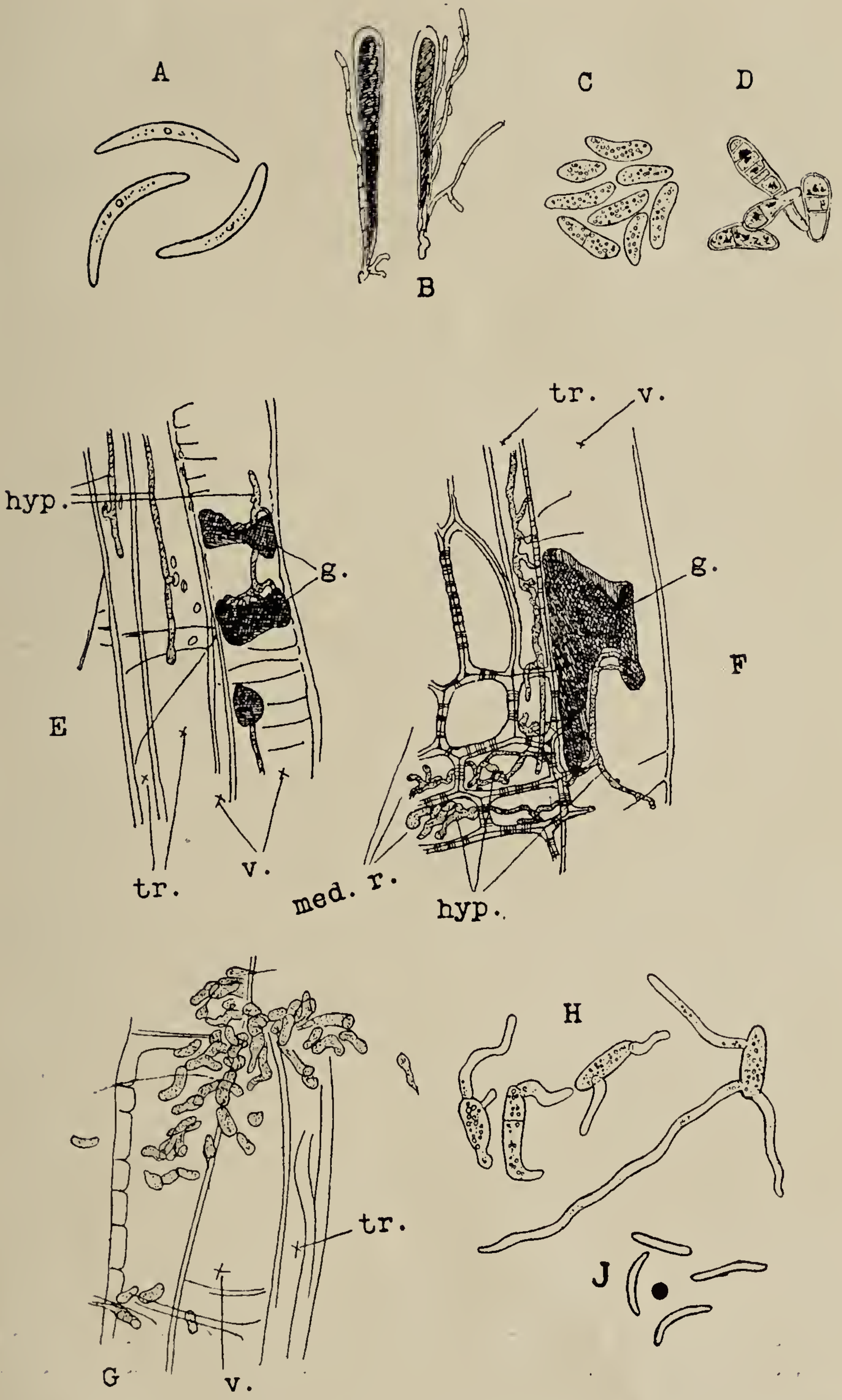

Fig. 3. *Dermatella prunastri* Pers. A, conidia from a naturally formed pycnidium in glycerine. B, young asci and paraphyses in lactophenol and "Bleu coton G 4 b." C, ejected ascospores. D, germinating ascospores killed in chrom-acetic acid and stained in Heidenhain's iron-alum hæmatoxylin. E, F, mycelium in the wood, stained in methyl green and Congo red; hyp., hyphæ; g., gum; tr., tracheid; v., vessel; med. r., medullary ray. G, mycelium in the wood breaking up into oval bodies; stained in methyl green and Congo red. H, ascospores germinating on grape-juice agar. J, conidia from pure cultures. A, G, J, ×1200; C, D, H, ×690; B, E, F, ×430.

solution. All the dead and the greater part of the discoloured tissues were found to contain hyphæ which were most abundant a short distance behind the junction of discoloured and healthy tissue. Behind this area the hyphæ appeared to retreat from the wood to the cortical tissues for purposes of reproduction. The amount of gum in the tissues that had been dead some time was less than in those which were situated at the line of demarcation between healthy and unhealthy tissues. It would appear that gumming proceeds a little in advance of the hyphæ, a phenomenon also observed by Brooks[1] in Plum trees attacked by *Stereum purpureum.* This is in accordance with the well-known fact that Plum trees produce quantities of gum upon injury.

The amount of gum produced was so great in some junction areas which took the form of a fairly flat and oblique plate and not a central elongated cone, that in longitudinal sections the gum floated out as long (2—3 mm.) ribbonds and cylinders. The vessels in these areas were completely blocked by the long plugs of gum. The presence of the parasite no doubt causes the gumming in the vessels and tracheids; but it is the actual gum which kills the branch by stopping the transpiration current. The mycelium is to be found in all the elements of the wood, but especially in the vessels and medullary cells; it also occurs in the pith and cortex. In those cases where a diseased central cylinder is present the mycelium appears to travel rapidly up the pith in a similar manner as described by Brooks and Bartlett[2] in the case of *Botrytis* attacking Gooseberry bushes. The hyphæ pass in a horizontal direction into neighbouring tracheids and vessels through the simple or slightly bordered pits, and also in the medullary ray cells in like manner (Fig. 3, E, F); but do not bore through the walls, which are not delignified.

A curious feature of the mycelium was noticed in those diseased areas where the hyphæ were most abundant. Some of the hyphæ had broken up into a number of small oval-shaped bodies which were present in great numbers. In the cutting of the sections masses of these oval bodies were scattered up and down the vessels by the action of the razor and subsequent treatment. So far I have been unable to discover what function these bodies perform, but would suggest that they are the result of the disintegration of the hyphæ, owing to the age or lack of nourishment, or both (Fig. 3, G).

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[1] "Silver Leaf Disease." Journ. Agric. Soc., 1911-1912.

[2] "Two Diseases of Gooseberry Bushes." Annales Mycologici, vol. 8, No. 2, 1910.

As before mentioned, in the quite dead distal parts the mycelium retreats to the cortex to produce there the pycnidia and apothecia. A small portion of such a branch, 1 cm. in diameter and 1 cm. long, stripped of bark so as to have a narrow cylinder of cortex, was placed in a test tube which contained a pad of cotton wool saturated with sterilised water at the bottom. The tube was afterwards carefully plugged with wool. After some weeks pycnidia appeared from the remains of the cortex. One of these pycnidia at the time of writing was extruding a thread of conidia (cf. pure cultures).

VI.—PURE CULTURES.

It was found very difficult to obtain clean cultures of *Dermatella prunastri* in any quantity from the conidia chiefly owing to the fact that only a very small percentage of the conidia germinated. In order to make sure of obtaining a few conidia which would germinate a number of hanging-drop and plate cultures were made. The germination and growth into mycelia were observed in a few instances; but as these did not exceed more than three in number it has been thought advisable not to describe these till such cultures have been repeated. Suffice it to say that the conidia germinate at their ends by producing germ tubes which soon branch. The subsequent mycelia produced were similar to those formed in hanging-drop cultures of the ascospores to be presently described.

Ascospores in a pure state were obtained by placing detached apothecia into a drop of agar situated on the *bottom* plate of a damp-chamber slide. The asci discharged their spores upwards into the air of the chamber, the spores adhering to the glass cover slip forming the roof of the damp-chamber. The ascospores were discharged continuously for three days, and on examination it was found that many young and ripe asci were still present so that the apothecia in all probability take some days to completely discharge all their ascospores.

In the manner described above ascospores in great numbers were obtained. Although many of the groups of discharged ascospores were eight in number (Fig. 3, C), yet groups from all numbers from one to many hundreds were observed.

No doubt the aggregation of the spores in large numbers was determined by the surface energy of the film of moisture present on the cover-glass on to which the spores had been shot. From these discharged ascospores clean cultures were made, some of which were transferred to damp chambers for the purpose of watching the germination; others were plated on various media, and still others sown upon sterilised blocks of greengage wood and strips of bark. In hanging-drop cultures of grape-juice agar germination took place within twelve to twenty hours. Germ tubes were put out in succession at or near both ends of the spores (Fig. 3, H), the second germ tube appearing some time after the first had reached a considerable length.

Nearly all the ascospores sown in damp chambers germinated, and the first plates of a culture series were in a few days covered with small colonies. A brown pigment specially noticeable on the light coloured grape-juice agar was produced by the developing mycelia. The colonies did not extend over an area more than $\frac{1}{3}''$ in diameter, but became very much heaped up. They were yellowish brown in colour. At the edge of each colony was a distinct blue-black metallic glistening border, from which diffused the brown pigment which stained the medium in the immediate neighbourhood. The heaped up portion which consisted of a tangle of short-celled hyphæ bore minute drops of extruded liquid of a brown colour upon its upper surface which seemed to indicate some kind of metabolic activity going on within the mycelium and possibly associated with the formation of fruit-bodies (cf. pure cultures).

In one experiment a germinating conidium was transferred from a damp chamber to a Petri dish at the same time as two germinating ascospores. The three mycelia which arose from these spores were exactly similar in appearance, the conidium producing a mycelium of the same characteristic form as the mycelia obtained from the ascospores. In old plate cultures in which the agar had dried to a thin skin presenting flattened colonies, were found small stumpy pycnidia which contained the sickle shaped conidia similar to those formed in nature, but rather smaller (Fig. 3, J).

The ascospores were also sown upon sterilised blocks of greengage wood; but time did not allow of these cultures being followed up. Cultures of mycelia obtained from ascospores and transferred from plates of agar to sterile blocks of greengage wood and bark, produced mycelia which spread slowly over the surface of the wood. After six weeks' growth the whole of one side of a block of wood was covered with an aerial mycelium consisting of short lax hyphæ yellowish in the older parts and white where newly formed. The mycelium was more luxuriant and spread faster on the bark than upon the wood. In these bark cultures it was noticed that the mycelium originally placed upon the outer surface, appeared next on the inner surface of the block (a small zone of wood was always left on the bark strips), indicating the penetration of the hyphæ in a radial direction. In one culture in which the block of wood was split down the centre so as to contain some of the pith, the mycelium extended both ways on the pith more rapidly than upon the wood. In all these cultures after three weeks' growth pycnidia were produced, some of which were of the normal type, others, however, resembled the apothecia in appearance and were flattened structures in various stages of development. The youngest consisted of a boss of pseudo-parenchymatous tissue surrounded by a felt-like mass of yellowish-green hyphæ from the ends of which the conidia were abstricted. The majority of the conidia were about half the size of those formed in nature and not so markedly crescent shaped; a fair number, however, exactly resembled the normal conidia (Fig. 3, A, J).

VII.—INOCULATION EXPERIMENTS.

During the cultural work several inoculations were made on young greengage trees in the University Botanic Gardens. Inoculations with pieces of diseased wood and with pure cultures of mycelia were carried out in December and January. In each case control inoculations were made with (*a*) sterilised pieces of diseased wood, (*b*) pieces of sterile agar. The inoculations were made at various places on both young and old branches. In (*a*) a hole was cut in the branch the same size as the diseased piece of wood which was in the shape of a small rectangular block; in (*b*) a T-shaped wound was made under the flaps of which the mycelium or agar was inserted. The wounds were afterwards covered with tinfoil and bound round with wool.

An inoculation and its control made upon the 21st January, 1913 was examined upon the 5th March, 1913. No discolouration beyond the surface of the wound was observed in the control; but in the inoculation with mycelium obtained from acrospores a slight discolouration was observed in the immediate neighbourhood of the wound. A fair amount of gumming had taken place and hyphæ similar to those in nature were present in the wood. It seems probable, therefore, that *Dermatella prunastri* is the parasite which causes the "die back" of greengages described in this paper.

Infection of the greengage trees in nature probably takes place through wounds on the young shoots. As *Dermatella prunastri* is only found to any extent upon greengages and occurs very rarely upon other plum trees it is of economic importance only in regard to the former upon which it may work considerable havoc in the course of time. As a remedial measure it is suggested that all branches upon which the pycnidia and apothecia of *Dermatella* are observed should be cut off some distance below the most proximal positions of the fructifications and burnt. The fungus spreads slowly, hence pruning of the kind suggested should check it effectively.

SUMMARY.

The results so far obtained may be thus summarised :—

(1). *Dermatella prunastri* Pers. has been grown in pure culture from conidia and from ascospores. (2). The mycelia arising from both these kinds of spores when growing on nutrient agar and sterilised pieces of greengage wood and bark produced pycnidia after some three weeks' growth. (3). The mycelium was found present in all the tissues of the host and particularly in the wood and pith. (4). The vessels, tracheids, and fibres are not delignified and the hyphæ pass from one cell to another by way of the pits. (5.) The mycelium advancing up a branch is preceded by gumming in the woody elements. (6). The inoculations of healthy greengage trees with the mycelium of *Dermatella prunastri* led to infection.

ON THE PRESENCE OF CONNECTING THREADS IN GRAFT HYBRIDS.

BY MARGARET HUME,

Late Bathurst Student of Newnham College, Cambridge.

[WITH ONE FIGURE IN THE TEXT.]

HISTORICAL.

THE genesis of connecting threads has long been a subject of discussion and it still remains an open question whether they arise from the spindle-fibres and perforate the cell-wall ab initio or whether they may be formed subsequently. The possibility that both methods occur, of course, is not excluded.

It was Tangl (14, p. 182) who first noticed that the connecting threads between the cells of certain endosperms resemble very strongly the striations which connect the endosperm nuclei during their division in the embryo-sac and hence arose the view that connecting threads originate as spindle-fibres and perforate the cell-wall from the time of its origin, a view shared by Russow (12,

p. 14) and by W. Gardiner (6, p. 110; 7, p. 187) and A. W. Hill (8, p. 282). The opposite view is upheld by Kienitz-Gerloff (9, p. 40) and by Strasburger (13, p. 493). The latter devotes the greater part of a long paper on "Plasmaverbindungen" to the citation of evidence in support of his view. The question is there very fully discussed and the literature quoted. A great number of cases is mentioned in which connecting threads occur between cells which almost certainly have only a very remote genetic connexion, but in no instance can this be shewn to be quite conclusively so. Could cells be found which were linked by connecting threads but which were known to be of different genetic origin, a theory of the formation of connecting threads from the spindle-fibres exclusively could not be any longer upheld. Even before the recent views with regard to graft hybrids had been developed, attention had been directed towards grafts as possibly offering suitable material for an investigation. The point where a graft is united with the stock is a region where tissues of different genetic origin are in living continuity, but the differentiation between the tissues of stock and scion cannot be easy and observations of connecting threads recorded between such tissues can scarcely be accepted as conclusive. Strasburger (13, p. 584 *et seq.*) describes connecting threads formed between the tissues of *Abies nobilis* and *Abies pectinata*, in such circumstances, and gives a figure (13, pl. xiv, fig. 10), but Arthur Meyer (11, p. 105) records his inability to find any means of distinguishing between the tissues of stock and scion.

The artificial production of graft hybrids of *Solanum lycopersicum* and *Solanum nigrum* by Winkler (15, 16, 17, 18, 19) and the interpretation of them as periclinal chimæras by Baur (1, 2, 3) has supplied new material for the study of connecting threads between genetically unrelated tissues. There seems no reason to doubt that Baur is right in his explanation and that, for example, Winkler's *Solanum tubingense* is actually *Solanum nigrum* in an epidermis of *Solanum lycopersicum*, and that *Solanum Kœlreuterianum* is *Solanum lycopersicum* in an epidermis of *Solanum nigrum*. The theory is also applied to the long familiar graft hybrids *Cytisus Adami* (4; 10, p. 268) and *Cratægomespilus*.

THE PRESENT RESEARCH.

The most suitable of the graft hybrids for the purpose of a histological examination seemed to be *Cytisus Adami*, *Solanum tubingense* and *Solanum Kœlreuterianum*, since in these the epidermis is the only layer of cells belonging to the one component, and the line of demarcation between the two components is therefore a sharp one. In *Cratægomespilus* and in some of the other *Solanum* graft hybrids, more than one of the outer layers of cells belong to the one component, and as the cells under the epidermis are not regularly arranged, it is impossible to say with absolute certainty to which component any one cell may belong, a state of affairs which makes these graft hybrids quite useless as a basis for argument upon the genesis of connecting threads.

When the present investigation was begun, the writer was unaware that the existence of connecting threads had already been demonstrated between the two components (*Cytisus purpureus* and *Laburnum vulgare*) of *Cytisus Adami.* This has been done by Buder (5, p. 214) and it only remains for the writer to confirm his observation of the connexion between the epidermis and the layer below it, by means of deep pits.

The material of *Cytisus Adami* was obtained from the Royal Botanic Gardens, Kew, and the material of *Solanum tubingense* and *Solanum Kœlreuterianum* from the John Innes Horticultural Institute at Merton.

The methods used were the ones generally employed for the demonstration of connecting threads. The material was fixed in a dilute iodine solution and mordaunted in a mixture of potassium iodide and uranium nitrate; it was then cut on the freezing microtome, stained in safranin and washed out with dilute glycerine and London blue.

1. *Cytisus Adami.* To ensure that the tissue used was really that of *Cytisus Adami* and not material from any part of the graft hybrid, which might have reverted to one of the original components, a part of the flower was chosen, for it is in the flower that the characteristics of *Cytisus Adami* are most sharply distinguishable. The actual part of the flower used, was the thickened base of the vexillum, where it narrows down to the point of attachment.

As has already been stated, the results obtained for *Cytisus Adami* were confirmatory of those obtained by Buder. Deep pits connect the cells of the epidermis with those of the underlying layer, but Buder (5, p. 214, text-fig. 1) depicts numerous delicate threads crossing the pit-closing membrane, which the present writer was unable to distinguish with certainty, though their presence is naturally to be suspected. The pits and their fillings do not differ in appearance from those which connect the cortical cells of *Cytisus Adami* with one another.

2. *Solanum tubingense.* In this graft hybrid which has the epidermis of the tomato (*S. lycopersicum*) and the sub-epidermal tissues of the black nightshade (*S. nigrum*), the connecting threads between the epidermis and the underlying layer of cells, are demonstrated very easily. The material used was taken from the stem of a part of the plant which showed the typical hairy tomato epidermis and the leaf-shape and other characters of the nightshade. The threads connecting the epidermal cells with those of the layer below correspond exactly with those connecting together neighbouring epidermal cells or neighbouring cortical cells. The threads are not situated in pits though the cell-walls are generally rather thinner in the regions perforated by the threads, but the thinning of the wall is gradual and not abrupt as in pit formation (see Fig. 1). The median node of each thread is very marked and if the cell-wall is split along the middle lamella, the median node can often be seen to be split also, each half of the fractured thread retaining a dark dot upon the broken end. The only difference between the threads connecting the epidermis with the sub-epidermal layer, and the threads connecting epidermis or cortex inter se is the greater frequency of the latter.

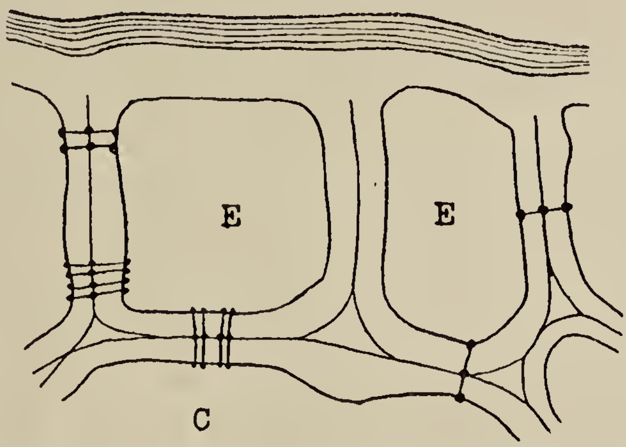

Fig. 1. *Solanum tubingense.* Transverse section showing connecting threads between epidermis (E) and cortex (C). × 1200.

3. *Solanum Kœlreuterianum.* This graft hybrid is the converse of the foregoing, it has the nightshade epidermis and the sub-epidermal tissue of the tomato. It was not found possible to demonstrate connecting threads in it at all, between any of the tissues. The material or methods of preparation must have been unsuitable for some reason, though in age and general character the material did not seem to differ from that of *Solanum tubingense* which gave such excellent results.

The negative result in the case of *Solanum Kœbrenterianum* does not however in any way invalidate the positive evidence yielded by *Cytisus Adami* and *Solanum tubingense,* since no connecting threads could be demonstrated anywhere, in tissues either related or unrelated.

CONCLUSIONS.

The principal conclusion to be drawn is, that if Baur's hypothesis is true, and there is every reason to believe that it is, and that graft hybrids really are periclinal chimæras, then there is no doubt that genetically unrelated tissues can be joined by connecting threads. The threads therefore arise secondarily, since it is to be supposed that the naked cytoplasm of the two components does not come into contact. At any rate it is clear that the threads cannot have arisen from spindle-fibres, since no nuclei of the two components have ever been sisters.

The breaking of the threads right across the centre of the median node when the middle lamella is split, is rather suggestive of a dual origin of the threads, half coming from the cell on either side. The median node is the thickest part of the thread and so presumably the strongest, and unless there were a division or joint running across it, a break might naturally be expected to occur at one of the thinner parts on either side of the median node. It must however be recalled in this connexion that some doubt exists as to whether connecting threads in the mature plant-cell are ever absolutely continuous across the middle lamella (8, p. 282).

The foregoing results do not in any way necessitate the supposition that connecting threads are always secondary and cannot arise from the spindle-fibres, though that view is rather indicated, at any rate for ordinary ground-tissue, because the connecting threads joining cells of genetically related and cells of genetically unrelated tissues are to all appearances entirely the same.

The research was begun while holding a Bathurst Studentship of Newnham College. The writer is indebted to Professor Seward for kind permission to work at the Botany School.

BOTANY SCHOOL,
CAMBRIDGE.
April, 1913.

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REVIEW.

A COLONIAL CONTRIBUTION TO OUR KNOWLEDGE OF THE GENUS *LYCOPODIUM.*

IN 1909 Mr. Holloway (3) contributed to the Transactions of the New Zealand Institute a very interesting account of six species of *Lycopodium.* As these Transactions are not within the reach of all British botanists it was thought that some account of Mr. Holloway's work and comments on his conclusions might be welcome.

In the first place Mr. Holloway has made a notable contribution to our knowledge of that puzzling organ, the protocorm. A protocorm was found in two only of the species he examined: in *Lycopodium cernuum* L. in which its structure was already well known and in *L. laterale* R. Br. In the latter species the protocorm is associated—as in the other cases in which it has been found, not only in *Lycopodium* but in *Phylloglossum*—with a prothallus of the *Lycopodium cernuum* type; the only exception to this generalization is the rudimentary protocorm recorded by Treub for *L. Phlegmaria.* In *L. laterale* the protocorm as described by Mr. Holloway is a comparatively highly developed organ. Instead of giving rise relatively early to the stem it elongates laterally to form a sort of rhizome bearing numerous protophylls on its dorsal surface; in a case figured there are as many as nine of these. Further this "rhizome" may branch and each branch may give rise to a stem, the stem apex being in all cases differentiated by the aggregation of the protophylls at a certain point on the dorsal surface of the "rhizome." The first root arises very late as an outgrowth of the latter.

In *Phylloglossum* the protocorm or tuber seems to play an even more important part than in *Lycopodium laterale*; yet the only trace of vascular tissue recorded in it is a ring of somewhat degraded xylem found by Mr. Wernham (7) in one portion of a single tuber of *Phylloglossum.* This lends great interest to the following passage from Mr. Holloway's paper: "Transverse sections of stems of young plants of these species (*L. cernuum* and *L. laterale*) at this stage show that there is no definite arrangement of the vascular tissues, the different xylem and phloem elements preserving no constant relative positions. The vascular tissues of the stem lead down bodily into the upper region of the protocorm, and, surrounded by a slight zone of sclerenchyma, enter the root-like protuberance, in the case of *L. laterale* passing along the dorsal surface of the protocorm immediately beneath the epidermis." It is not quite clear from this passage whether the vascular elements passing downwards from the stem enter a root-like protuberance in both species or only in *L. laterale.* Presumably this is so only in *L. laterale* as the examples of young protocorms of *L. cernuum* figured show no root-like projections in their upper parts, into which alone it is stated that the vascular elements extend.

Mr. Holloway keeps an open mind on the vexed question as to whether the protocorm is a late specialization or a highly primitive organ. He remarks that at first sight the case of *L. laterale* might seem to afford an argument in favour of the latter view, for the protocorm here "by no means bears the character of a mere temporary organ"; but he adds that it might be urged with considerable reason that the "protocormous rhizome" of *L. laterale* may be "merely a physiological specialization, peculiar to this species," designed to carry this marsh-loving form over an unsuitable season. Without entering fully into the difficult controversy concerning the nature of the protocorm it may be well to recall that Professor Bower in his later works regards the protocorm not as a persistent relic from a remote ancestry but as a parenchymatous swelling of the nature of an opportunist growth; he compares it to the foot, drawing the conclusion that the Lycopod embryo seems prone to parenchymatous swelling (2). Other writers hold the view, first set forth by Treub, that the protocorm is the phylogenetic precursor of the stem, a view once also held by Professor Bower (1, 6, 7). In the face of Mr. Holloway's demonstration that vascular tissue penetrates for some distance in the protocorm of *L. laterale* this organ cannot, at least in that species, be dismissed as a mere parenchymatous swelling. Further, it is difficult to deny the probability that the protocorm of *L. laterale* had the same origin as those of *L. cernuum* and *L. inundatum*, for all three species show close relationship in their prothalli and general structure. But are we, therefore, bound to accept the protocorm as the primitive form of the stem, the precursor of the ordinary form of Lycopodinous axis? I think not. It is true that Dr. Lang has shown that the type of prothallus with which the protocorm is associated is probably primitive and there seems an inherent probability that the gametophyte, often relatively long-lived, might influence the embryology of the young sporophyte. But in the face of the enormous development of the stem in the oldest fossil Lycopods known to us and of the essential histological similarities of the stem throughout the phylum of the Lycopodiales the probability that the protocorm is a modified form of stem, due to reduction, at once suggests itself and this view is supported by the late development of vascular tissues in the Lycopodiaceæ. If the protocorm is a reduced form of the stem it is quite natural that in *L. laterale* where this reduction is much less than in the other species of *Lycopodium* some vascular tissues should persist. It is, of course, possible to regard the protocorm of *L. laterale* as the last term in a series of swellings, at first parenchymatous in nature but later developing vascular tissue in accordance with their opportunist nature. But that stems may by shortening and reduction assume a protocorm-like form is shown among the Pteridophyta by the recently described case of a protocorm in *Ophioglossum vulgatum* (6). This protocorm has, it is true, little in common with that of the eligulate Lycopods except outward form; for it is provided with a vascular system comparable in all essentials to that of the rhizome, except that owing to unequal growth of the upper and lower parts of the segments of the apical cell the vascular system has become turned inside out and everted, the apical region having been displaced through the centre of the stele "as one would pull the bottom of an inverted sack through the tubular part" (6).

Passing to the anatomical structure Mr. Holloway distinguishes two main types in the young stem. In the one the first vascular elements to develop in the stem are those of the leaf-traces; later the latter affix themselves irregularly to the vascular elements formed from the plerome cylinder; in this type, found in *L. cernuum* and *L. laterale*, xylem and phloem are irregularly intermingled. In the second type found in *L. Billardieri*, *L. volubile* and *L. scariosum*, the vascular elements of the plerome cylinder develop before those of the root and leaf; here the structure of the stele is more compact and definite, and the leaves, fewer in number, are more regularly arranged. In the mature stem Mr. Holloway also recognises two main types, the "mixed" and the banded. In the latter type he includes two very distinct forms: those in which the bands of xylem and phloem are arranged more or less radially and those in which these bands are more or less parallel to one another, except where the attachment of the roots causes some disturbance. Mr. Holloway considers that the type of stele showing parellel arrangement of the xylem and phloem is especially characteristic of plagiotropic stems and concludes that it arises as a modification of the type with radial bands of vascular tisssue, owing to the restriction of branching to one plane in these plagiotropic forms· In this he is in general agreement with Mr. Jones (4, p. 27) and Miss Wigglesworth (9), and the probability is that this view would be generally accepted. But Mr. Holloway's further contention that the banded types thus grouped together are less primitive than the "mixed" type is open to many objections. In the first place the more regular arrangement of the type showing radial bands (of which Mr. Holloway himself considers the type with parallel bands merely a variety) is much more easily brought into line with the steles of the older fossil Lycopods and of the simpler species of *Selaginella*; indeed the radial type of stele which is found in the roots of the Pteridophyta generally seems to be as old as the circular protostele. The "mixed" type on the other hand seems to be peculiar to certain species of Lycopodium and if we regard it as primitive for the genus we must either assume that it originated from a protostele and gave rise to the type with radial bands of vascular tissue which it would seem more natural to derive directly from the protostele; or we must regard the stele of *Lycopodium* as having originated independently of the stele of other Lycopods, recent and fossil; this last solution of the difficulty seems very unnatural, for the stele of this genus agrees very closely in its histology with those of the other members of the phylum. Again we may note that in the "mixed" type the purely cauline part of the stele is less differentiated and in the young sporophyte the leaf-traces contain the first vascular elements, whereas in the banded types the purely cauline elements develop first. In a phylum of which the relatively great development of the stem compared with the leaf is one of the principal characteristics it is natural to regard the latter condition as primitive. Mr. Holloway seeks to support the primitiveness of the "mixed" stele by urging that the more definite arrangement found in *L. Billardieri*, *L. volubile* and *L. scariosum* was made possible by the diminution in number of the leaf traces consequent on the adoption of a subterranean habit by the prothallus and young plant. He considers, too, that the well developed sclerotic region of the cortex of these three species, a region absent from *L. cernuum* and feebly developed in *L. laterale* may by enveloping the developing stelar tissues serve to insure greater cohesion of the xylem elements into groups and bands "by imparting rigidity and lateral pressure to the tissues." These conjectures, however, as to the causes of the changes supposed to have taken place can hardly have the same weight as generalisations founded on a comparison with the stelar tissues of other members of the Lycopodiales.

ISABEL M. P. BROWNE.

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RECENT WORK ON FLAGELLATA AND PRIMITIVE ALGÆ.

By F. Cavers.

(Continued from p. 187),

IX.—Conclusion.

WHILE the recent work summarised here has led, through the discovery of interesting new species and genera and the re-investigation of forms previously known imperfectly, to a clearer knowledge of the Brown Flagellates and of the relations between these and the Brown Algæ, it has thrown little further light upon the phylogeny of the Green Algæ. The possibility that the Cryptomonads are related to the Chlamydomonads has been discussed by Fritsch (46), who admits, however, that the origin of the flagella from a depression and the obliquity of the cell in the Cryptomonads is against the view of a really close relationship. However, the Chrysomonadineæ and the lowest Chlamydomonads—the Polyblepharidaceæ—may well have arisen from a common ancestral form, which we may imagine to have been multiflagellate and amœboid, with a basin-shaped chromatophore. Apart from the differences in flagellum number and the nature of the assimilate we fiind corresponding simple "mastigamœboid" forms in each of the orders of Chrysomonadineæ—e.g., *Chrysamœba*, *Hymenomonas*, *Ochromonas*, *Wysotzkia*; while the Chloromonad genus *Chloramœba* suggests the origin of the Chloromonadineæ from a similar ancestral form by the division of the primitively single basin-shaped chromatophore into a number of small chloroplasts. If the multiflagellate condition is taken as primitive, we must regard the Polyblepharidaceæ, which also have a limited power of change of shape, as being nearer to the ancestral stock than any of the other coloured Flagellate and lower Algal forms.

The nearest approach to such an ancestral form is the colourless *Multicilia*, with two species, of which *M. lacustris* is multinucleate while *M. marina* has a single nucleus; in both species, the spherical body bears numerous radiating flagella, food is ingested by pseudopodia which may be put out from any point, there are numerous peripheral contractile vacuoles, and division occurs by median constriction of the body as in *Amœba*. Probably the primitive form of chromatophore was a reticulate peripheral sheet immediately within the periplast, and when the flagella became restricted to the anterior end of the body this sheet would become basin-shaped (*i.e.*, open anteriorly) as in the majority of Volvocales and in various Chrysomonads, or on the other hand broken up into numerous small chromatophores, as in Chloromonadineæ, *Glœomonas* (allied to Chlamydomonas), *Chrysococcus dokidophorus* (Chromulinales), etc. A reticulate chromatophore occurs in *Chrysapsis* (one of the most primitive Chrysomonads), and in certain Volvocales (*Sphærella*, *Chlorogonium*). The bell-shaped chromatophore which is characteristic of the Volvocales and of the simpler Chrysomonadineæ has undergone longitudinal splitting in at least one genus (*Scherffelia*) in the former group and in the majority of the Chrysomonadineæ, giving rise to two lateral curved band-like chromatophores; these two types of chromatophore may occur in different species of the same genus, as is seen in *Uroglenopsis* (Ochromonadales).

If, while bearing in mind Vuillemin's timely caution against dogmatism in such matters, we assume that autotrophic organisms are primitive and heterotrophic organisms derived, and that the Flagellata represent the most primitive organisms known to us, the striking parallism which has been shown to exist between the Brown Flagellates and certain colourless Flagellates suggests the view that the whole of the latter may have arisen from coloured autotropic forms by adaptation to heterotrophic modes of nutrition. On this view, the classification of the Flagellata which has hitherto been accepted is purely physiological, and therefore artificial, corresponding with the conventional division of the Thallophyta into Algæ and Fungi; and the various groups of colourless Flagellates will doubtless be shown, on further investigation, to have arisen from corresponding forms among the coloured Flagellates, just as the various groups of Fungi are now regarded as arising from corresponding Algal forms. Of the many lines starting from a hypothetical autotrophic *Multicilia*-like ancestral form, with a reticulate chromatophore, numerous peripherally situated nuclear bodies, and numerous flagella, some have ended blindly and produced nothing higher than Flagellates—a few of these remaining autotrophic but the majority becoming adapted to various modes of heterotrophic nutrition—while three may be traced into the Vegetable Kingdom and lead respectively (i) through the Polyblepharids to the Chlamydomonads and thence to the majority of Green Algæ, (ii) through the Chloromonads to the Confervales, and (iii) through the Chrysomonads to the Cryptomonads and thence to the Phæophyceæ, the Peridiniales, and probably the Diatoms.

The origin of the remaining Algal groups from Flagellata is much more difficult to trace, owing to the absence of transitional forms. There are no forms whatever which would serve to connect the Blue-green and the Red Algæ with the known Flagellates of corresponding colour; it is much more likely that the Cyanophyceæ are related to the Bacteria, while the Rhodophyceæ may have been derived from the same stock as the Dictyotaceæ, which occupy a somewhat isolated position among the Phæophyceæ. The origin of the Diatoms is an equally open question; it seems likely, at any rate, that they are related to the Peridiniales or to the Chrysomonads rather than to the Conjugatæ.

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THE PROBLEM OF THE ORIGIN OF *ŒNOTHERA LAMARCKIANA* DE VRIES.

BY BRADLEY MOORE DAVIS,
University of Pennsylvania.

[WITH ONE FIGURE IN THE TEXT].

I am led to write this paper partly for the reason that the problem of the origin of *Œnothera Lamarckiana* De Vries has in the past few months became far more tangible than formerly, but chiefly because it seems probable that certain phases of the problem can be solved only by studies on the development of certain English *Œnothera* floras. I have then the hope that a brief outline of the situation, as it now appears to me, will be of some assistance to British botanists interested in the subject.

Recent studies[1] clearly indicate that the *Lamarckiana* of the cultures of De Vries cannot be identified with the plant described by Lamarck[2] under the name *Ænothera grandiflora* from material grown in Paris at about 1796 or earlier and renamed by Seringe[3] *Œnothera Lamarckiana.* The evidence is very strong that Lamarck's plant (*Œnothera Lamarckiana* Seringe), was a form of *Œnothera grandiflora* Solander[4] (*O. grandiflora* "Aiton") introduced into England in 1778 from Alabama.

This disposition of *Œnothera Lamarckiana* Seringe as a form of *O. grandiflora* Solander relieves our problem from association with the early date of 1796 and allows us to pass to later periods when we may hope for more direct evidence than that furnished by old descriptions and figures. The attempts to establish the presence of *O. Lamarckiana* De Vries in Europe at dates previous to 1796 are, to the writer, not convincing and have been discussed in previous papers.[1] In a recent contribution Gates[2] abandons his former views and admits (pp. 17-19) that the presence of *Lamarckiana* in Europe previous to 1760 is not established.

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[1] Davis, B. M. "Was Lamarck's evening primrose (*Œnothera Lamarckiana* Seringe) a form of *Œnothera grandiflora* Solander?" Bull. Torrey Bot. Club, vol. 39, p. 519, 1912.

[2] Lamarck. Encyclopédie Méthodique Botanique, vol. 4, p. 554, ? 1798.

[3] Seringe, N. C. De Candolle, Prodromus, vol. 3, p. 47, 1828.

[4] Solander, D. Aiton, Hortus Kewensis, vol. 2, p. 2, 1789.

Since *Œnothera Lamarckiana* Seringe becomes a synonym of *O. grandiflora* Solander, I have proposed that the plant of De Vries retain the name under which it is known in the extensive literature of experimental morphology, but the name must be written *Œnothera Lamarckiana* De Vries. In making the above suggestion it should be noted that *O. Lamarckiana* De Vries has come down to us as the product of the garden through a long history of cultivation and that there are good reasons for believing it to be of hybrid origin. We have no evidence that the plant is present as a native species of any flora. As a garden plant we are apparently justified in giving it the name *Œnothera Lamarckiana* De Vries by Article 50 of the nomenclatorial code formulated by the International Botanical Congress held in Vienna in 1905.

There is little doubt that the material of De Vries's cultures was derived, possibly greatly modified, from certain plants placed upon the market by the seedsmen Carter and Company of London at about 1860. These plants were considered by Lindley to be *Œnothera Lamarckiana* Seringe, but we cannot accept this identification as correct. However, this opinion of Lindley gave the name *Lamarckiana* under which seedsmen are to this day selling a somewhat heterogeneous mixture of forms.

The description of the cultures of Carter and Company,[3] accompanied by an obviously inaccurate figure, gives us very little information on the plants. We are told that they were 3-4 feet high, very hardy biennials, and with flowers 4 inches in diameter. Carter and Company state that their plants came from seed received unnamed from Texas.

The problem of the origin of *Œnothera Lamarckiana* De Vries at present largely centers on the probable composition of the cultures of Carter and Company, and every effort should be made to bring forward evidence on the characters of these plants. The only information so far at hand apart from the unsatisfactory description and plate in "The Floral Magazine" is that furnished by a very important sheet in the Gray Herbarium of Harvard University. This sheet I shall again describe and figure in the hope that it may lead botanists to make a persistent search for herbarium material that may throw further light on the problem.

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[1] See Davis, American Naturalist, vol. 45, pp. 226-227, 1911, and vol. 46, pp. 379-380, 1912.

[2] Gates, R. R. "A Contribution to a Knowledge of the Mutating Œnotheras." Trans. Linnean Society, Botany, vol. 8, Part 1, 1913.

[3] The Floral Magazine, vol. 2, plate 78, 1862.

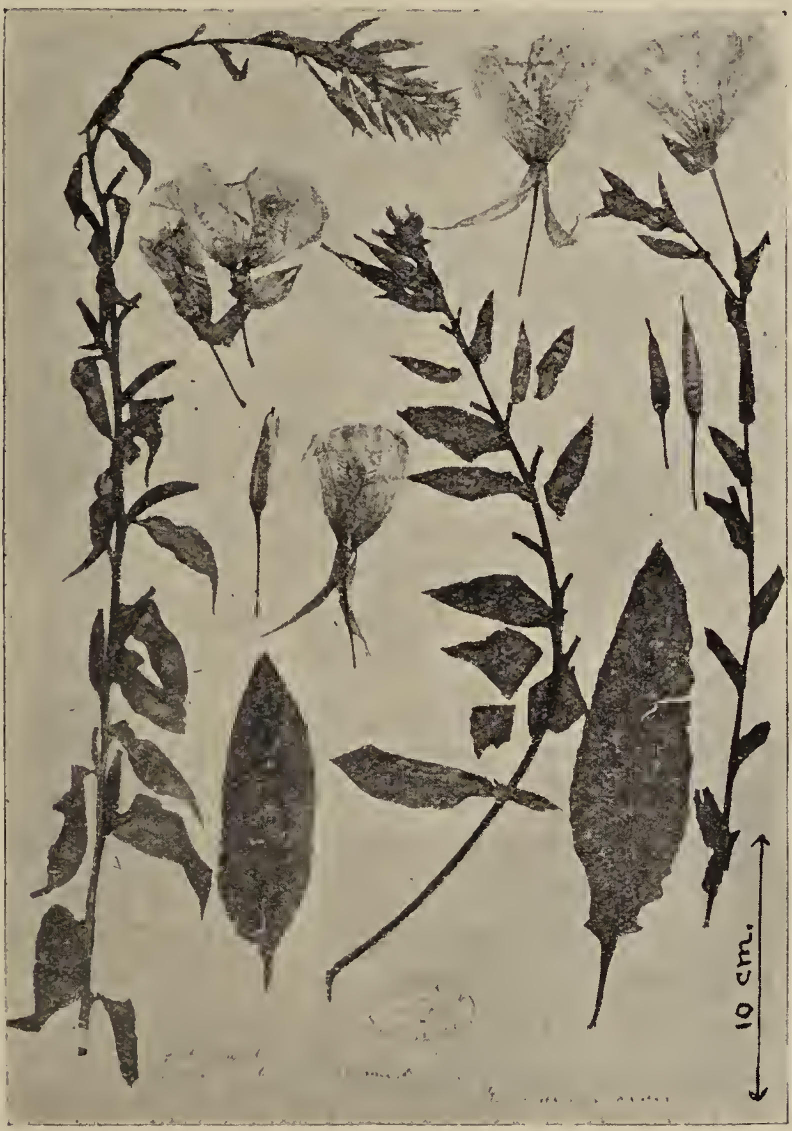

Fig. 1. Sheet in the Gray Herbarium of Harvard University. An *Œnothera* grown by Dr. Asa Gray at Cambridge, Massachusetts, in 1862 and probably derived directly or indirectly from the cultures of Carter and Company, of London, which were distributed under the name *Lamarckiana.* This plant differed from *Œnothera Lamarckiana* De Vries in the longer internodes of the inflorescence, in the larger and more leaf-like bracts, in the more slender form of the buds, in the more attenuated sepal tips, and in the longer seed-capsules.

The sheet in the Gray Herbarium (Fig. 1) holds specimens of a plant "*Oe. Lamarckiana*" grown in Cambridge, Massachusetts, in 1862 by Dr. Asa Gray. From records upon the sheet[1] it appears quite certain that Dr. Gray received seeds from William Thompson of Ipswich, England, a seedsman who probably obtained from Carter and Company their novelty. It is then possible that the plant grown by Dr. Gray was not more than one or two generations removed from the original cultures of Carter and Company. The following is a description of the sheet in the Gray Herbarium illustrated by Fig. 1 :—

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[1] See Davis, American Naturalist, vol. 46, p. 417, 1912.

1. *Stems and Foliage.*—The stem bears long hairs arising from papillæ which are colored red as in *Lamarckiana* and are about as numerous as in that species. The large detached leaf, about 18·5 cm. long with sinuate margins, slightly lobed below, and with some evidence of former crinkles, suggests by its shape (although too small) the basal leaves of *Lamarckiana*. The leaves of the upper foliage, short petioled, are not so nearly sessile as those of *Lamarckiana*.

2. *Inflorescence.*—The inflorescence has longer internodes than in *Lamarckiana* and consequently is not so compact. The bracts are broad at the base, slightly toothed, and persistent, becoming large, lanceolate leaves on the fruiting branches: those of *Lamackiana* remain much smaller.

3. *Buds.*—The buds are about 9·5 cm. long, not stout and 4-angled as in *Lamarckiana*. The sepal tips are more attenuate than in *Lamarckiana*, projecting 1 cm. beyond the folded petals. The pubescence upon the sepals consists of long hairs arising from papillæ among much shorter hairs as in *Lamarckiana*.

4. *Flowers.*—The petals are about 4·5 cm. long, as long as those of the largest forms of *Lamarckiana*. The stigma lobes are about 8 mm. long, and close to 5 mm. above the tips of the anthers, in these respects agreeing with large-flowered forms of *Lamarckiana*.

5. *Capsules.*—The capsules, about 3 cm. long, are longer than those of *Lamarckiana* and not so stout.

From the above it will be noted that the plant grown by Dr. Gray differed from the *Lamarckiana* of the cultures of De Vries in the longer internodes of the inflorescence, in the larger more leaf-like bracts, in the more slender form of the buds, in the more attenuated sepal tips, and in the longer seed capsules. It would profit little to discuss at present whether or not this plant was truly representative of the cultures of Carter and Company and whether or not their plants became greatly modified during the quarter century before the time when De Vries began his studies, at about 1886, and isolated the form that we know to-day as *Œnothera Lamarckiana* De Vries.

What we desire is further information on the composition of the cultures of Carter and Company through the discovery of other herbarium material of about the same date (1862) as that of the sheet in the Gray Herbarium. It will be strange if Dr. Gray proves to the only botanist who preserved specimens of the "Lamarckiana" placed on the market by Carter and Company. There should be made a persistent search through herbaria to bring forward any specimen that may throw light upon the problem. This is a matter in which it would seem that the British botanists can render a great service.

Another feature of the problem concerns the development of some remarkable *Œnothera* floras in parts of England composed in greater part of *O. Lamarckiana* or variants from this type.

It is surprising how common have become *Lamarckiana*-like forms in England. During the past three years several English botanists have kindly replied to my request for seed of broad-leaved forms of *Œnothera biennis* with green stems bearing red papillæ at the base of long hairs. From the seed sent to me I have grown eleven different cultures in the hope of finding a type of *biennis* which in the past I have greatly desired as a parent for a cross with *O. grandiflora*. All of these cultures have proved to be forms essentially *Lamarckiana* as to habit, foliage and stem coloration, but with smaller flowers than is usual for De Vries's plant. They correspond very closely and some of them are indistinguishable from the small-flowered races of *Lamarckiana* which I have differentiated from material of De Vries.[1] They were not at all the forms of *biennis* that I hoped to obtain, and could not be used in my experimental work.

The type of *biennis* that I wish should agree closely in morphology with the *biennis* of the sand dunes of Holland, but it should have the stem coloration characteristic of *Lamarckiana*, i.e., the green portions of the stems should be punctate with red papillæ at the base of the long hairs. The Dutch *biennis* has as far as we know a clear green stem above, but it would not be surprising if a form should be found with the stem coloration of *Lamarckiana*, since races of American *biennis* occur differing only in the presence or absence of red coloration in the stem papillæ. Seeds of a type agreeing with the Dutch *biennis* have been sent to me from the botanical garden of Cambridge University and presumably the plant is not uncommon in England. De Vries[1] reports (p. 32) that it is present on the sand hills of Lancashire.

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[1] See Davis, American Naturalist, vol. 46, p. 383, 1912.

This plant which I have referred to as the Dutch *biennis*, so well known through the studies of De Vries, is perhaps the most important type in the *biennis* assemblage of races and should be familiar to all students of œnotheras. It is very old having apparently been on the sand dunes of Holland since pre-Linnean times. Bartlett[2] has recently brought forward strong reasons for regarding the plant as the form known to Linnæus as *Œnothera biennis* and consequently to be regarded as the type-form of the species. It is very important that British botanists should endeavour to trace the history of this species in England and its relations to the present *Œnothera* floras. I shall be glad to supply seeds of the plant to anyone interested in the study.

To return to the specific problems of the origin and development of *Lamarckiana* floras in England the most important and historically the most interesting flora seems to be that of the Lancashire sand hills north of Liverpool. From the studies of several botanists it appears that over an extensive area *O. Lamarckiana* De Vries occurs mixed with variants from the type proper. It is reported by Gates (l.c. 1913) that *O. grandiflora* is also present with the *Lamarckiana* and we have De Vries's statement (l.c. 1912) that the Dutch *biennis* (*O. biennis* Linnæus) is in the same region. The studies of Gates (l.c. 1913) clearly show that among the types there is a large amount of hybridization and consequently a very complex mixture of forms differing among themselves in many respects.

We know that a conspicuous *Œnothera* flora was present on the sand hills of Lancashire before 1806,[3] and the problem is briefly the determination of its original character and the tracing of its modification or development down to present times. The account by Smith in the "English Botany" (1806) together with the accompanying figure of James Sowerby's indicate a biennial plant, 2-3 feet high, a stem "rough with minute tubercles," leaves broad and the lower decidedly crinkled, flowers with petals about 3 cm. long (if drawn natural size), and stigma lobes slightly above the tips of the anthers. There is no mention of red coloration in the stem tubercles which suggests a plant with green stems as in the Dutch

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[1] De Vries H. "Die Mutationen in der Erblichkeitslehre." Berlin, 1912.

[2] Bartlett, H. H. "The Delimitation of *Œnothera biennis* L." Rhodora, vol. 15, p. 48, 1913.

[3] English Botany, vol. 22, p. 1543, 1806.

biennis and if the petals were really no more than 3 cm. long the flower size was also closer to this species than to the large-flowered forms of *Lamarckiana*. On the other hand the stigma lobes figured somewhat above the tips of the anthers are in a position more like that in *Lamarckiana* than in the Dutch *biennis* where the stigma lobes lie below the tips of the anthers and pollination takes place before the opening of the bud.

In the third edition of the "English Botany" Syme[1] gives a description of "*Œnothera biennis* Linn." and states it to be "now perfectly established on the Lancashire coast, at Crosbie, near Liverpool, and occuring occasionally throughout Britain, but generally an outcast from gardens." The description of this plant is accompanied by a somewhat different figure from that in the edition of 1806, but the two figures agree in all essentials of structure. The figure and description indicate a plant 2-3 feet high, rosette leaves oblanceolate-elliptical 6 inches to 1 foot long, stem leaves elliptical 3-6 inches long, all leaves short petioled and with thick white midribs, repand denticulate; flowers with petals $1\frac{1}{4}$ to $1\frac{1}{2}$ inch or more across (about 3-4 cm.), stigma lobes figured somewhat above the tips of the anthers; "plants dull green, sub-glabrous, with the stem, calyces, petioles, midribs, and margins of the leaves more or less hairy." In this account, also, as in that of the first edition (1806) there is no mention of that stem coloration characteristic of *Lamarckiana*, i.e., red papillæ on green portions of the stem. This point together with the statement that the plant is dull green suggests the Dutch *biennis* but the large petals and the position of the stigma indicate a plant with flowers more like those of *Lamarckiana*.

It ought at least to be possible to determine through herbaria whether or not the "*Œnothera biennis*" described in the different editions of the "English Botany" is the same form or one similar to the Dutch *biennis* which probably represents the *Œnothera biennis* of Linnæus. It ought to be possible to obtain evidence through herbaria for or against the possibility of the presence in England of *O. Lamarckiana* De Vries at a date as early as 1806 or at least previous to 1860. There should be some direct evidence whether or not *O. Lamarckiana* was first introduced into England through the cultures of Carter and Company at about 1860 and whether or not its appearance on the sand hills of Lancashire is of an earlier or a later date.

[1] English Botany, Third Edition, vol. 4, p. 24, 1865.

I have certain views on the subject but my purpose is not to present them at this time but to plead that a strong effort be made to fix the approximate date of the appearance in British *Œnothera* floras of the *biennis* of Linnæus (probably represented by the Dutch plant) and of *O. Lamarckiana* De Vries. The characters that are likely to be most helpful in distinguishing these species on herbarium sheets are:—

1. The presence in *Lamarckiana* and absence in the Dutch *biennis* (so far as is known) of red in the stem papillæ. It must be borne in mind, however, that some races close to the *biennis* of Linnæus have the stem coloration of *Lamarckiana*.

2. The size of the petals, 4-4·5 cm. long in the large-flowered forms of *Lamarckiana* and 2-2·5 cm. long in the Dutch *biennis*. There are small-flowered races of *Lamarckiana* the petals of which are of about the same size as those in the Dutch *biennis*.

3. The position of the stigma 5-7 mm. above the tips of the anthers in the large-flowered *Lamarckiana* (open pollinated) and well below in the Dutch *biennis* (close pollinated in the bud). The small-flowered races of *Lamarckiana* sometimes present the stigma in a lower position more like that of the Dutch *biennis*.

4. The coloration of the sepals, sometimes streaked with red in *Lamarckiana* but normally green in the Dutch *biennis*.

De Vries has suggested that what I have termed the small-flowered forms of *Lamarckiana* may be hybrids between the large-flowered type and *biennis*, but it is also possible that they are variants from *Lamarckiana*, itself a hybrid. It seems most unlikely that Great Britain has no herbarium sheets that can throw light on these problems.

Most interesting from my standpoint is the problem of the first appearance in England of the progenitors of *O. Lamarckiana* De Vries. Were they certainly first introduced through the cultures of Carter and Company, about 1860, or were they in England and perhaps on the sand hills of Lancashire previous to this date? Is it possible that the plants of Carter and Company came not from Texas but from some part of England, perhaps from the very sand hills of Lancashire? There certainly should be in British herbaria some evidence on these questions.

It seems to be impossible to determine with exactness what are the forms under consideration in some of the descriptions published at dates of great importance to our problem, and that is why I have laid so much importance upon herbarium material.

Thus Don[1] described in 1832 "*Œ. biennis*" from "sand banks on the coast of Lancashire" and noted that it "is common in gardens and often escapes from thence into rich waste ground," but the statements "flowers large" and "delicately fragrant" are relative matters and we cannot be certain from this or other parts of the account whether the plants were nearest to *Lamarckiana* De Vries or to forms of *biennis* such as that from Holland (the *biennis* of Linnæus). Lindley[2] in 1833 gave an account of "*Œnothera biennis* var. *grandiflora*" and stated it to be "not uncommon in gardens." The figure of this plant shows petals drawn about 3.5-4 cm. long, as large as those of *Lamarckiana* De Vries, but a basal or perhaps a rosette leaf is too narrow for *Lamarckiana*, nor will it do for the Dutch *biennis* or for *grandiflora*. The bracts are figured broad at the base and sessile as in both *Lamarckiana* and *biennis*, but the inflorescence with long internodes is not as in those species but is more like that of *grandiflora*; the bracts, however, are not those of *grandiflora*. These contradictions are most puzzling, but may there not be specimens preserved at this period which will clear the obscurity.

I am aware that the *Œnothera* floras in other parts of England offer opportunities for investigation that should not be overlooked in the study of the problems presented in this paper. I have, however, confined my suggestions to the remarkable assemblage on the sand hills of Lancashire for the reason that this region seems to be best known and to have been under observation for the longest period.

[1] Don, George. A General System of Gardening and Botany, vol. 2, p. 685, 1832.

[2] Lindley, John. *Œnothera biennis*; var. *grandiflora*. Edwards's Botanical Register, vol. 6, p. 1604, 1833.

UNIVERSITY OF PENNSYLVANIA.
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THE CLASSIFICATION OF CONIFERS.

By W. T. Saxton, M.A., F.L.S.,

Professor of Botany at the Ahmedabad Institute of Science, India.

[With One Figure in the Text.]

I.—Introduction.

EVER since Hofmeister's classical researches on Conifer gametophytes, published in 1862, an ever increasing number of workers has gradually widened our knowledge of this interesting group. Strasburger, whose first Conifer work appeared in 1869, has been the most indefatigable of these workers, while in recent years very many contributions of much more restricted scope have appeared, dealing generally with only one genus at a time, and working out its life history in greater detail than was possible when a wider field was dealt with. One result of this greater specialization has been that, in elucidating the details of particular genera, the bearing of the facts on phylogeny and classification has often been lost sight of, although all such work has had as its nominal objective the clearing up of relationships, either within the group, or between the Conifers and other phyla, or both.

In spite of the numerous detailed investigations of the last twenty years, systematists still use, almost solely, obvious external features to delimit the various families within the Coniferales.

While phylogeny is the ultimate goal in questions of relationship, yet it is impossible to successfully approach the more complex phylogenetic problems until some sort of agreement is reached, or at least until a satisfactory basis is found, in regard to the less complex question of classification.

The object of the present communication is therefore to discuss the relative values of various characters, both obvious and more recondite, as indicative of natural relationships; to apply the results to working out a more natural classification of the group; and finally to suggest, somewhat tentatively, a scheme of phylogeny on the basis of the proposed classification.

It has long been recognised in the Angiosperms that "habit," which depends chiefly upon the form and arrangement of the stem and leaves of a plant, is of extremely little use in arriving at a clear idea of natural relationship. If examples were needed to emphasize this statement, one might point to the extreme variation within such a genus as *Senecio*, or within families such as Euphorbiaceæ and Rosaceæ; in each of these cases the leaves may be seen to be the most plastic organs of the plant; there may be, within undoubtedly natural families, both simple and compound, opposite and alternate, stipulate and exstipulate leaves, of almost every conceivable shape. Where only one type of leaf, or only one "habit" is found in a family, it is usually where the geographical range of the family is very limited, or is such as to expose the plants to only one type of climate, as in the Proteaceæ and in several tropical families. Among the Gymnosperms, the Gnetales offer a good example of the enormous differences in habit which may be found within a somewhat narrow circle of affinity.

To approach the same problem from the opposite direction, we have the well known constancy of vegetative characters in plants admittedly unrelated (or only distantly related), when these are grouped in certain habitats which offer very characteristic ecological conditions; as examples the best known are probably the trees of tropical rain-forests and the "bush" vegetation of the Mediterranean region, south-western Africa, and parts of Australia.

There does not seem any adequate reason for supposing that leaf form and arrangement have any greater fixity in the Conifers than they have in other plants, yet we still find systematists separating two so-called "tribes," Cupresseæ and Taxodeæ,[1] almost solely on the basis of whether the leaves and the cone scales are opposite or alternate.

While the more recondite characters of the genera concerned were largely unknown the leaf characters offered a convenient means of cataloguing the species, but now that the internal structure and development of the reproductive organs are known in a large proportion of cases, it is time that the principles upon which the limits of the tribes and families are based should be somewhat less seriously behind the present status of botanical progress.

II.—Characters Important in Classification.

In theory, though unfortunately not always in practice, it is generally conceded that the stability and fixity of plant parts or organs is more or less proportional to (*a*) their distance from the surface of the plant, and (*b*) their proximity to, or connection with, the reproductive structures. Applying this theory, we see that the least important characters of the plant to the systematist ought to be the superficial characters of the vegetative organs, including the shape and position of the leaves. These parts are by far the *most* important to the plant, physiologically, and for this reason are the most susceptible to adaptive changes. It may further be stated that (i) the superficial characters of the reproductive structures, and (ii) the internal anatomy of vegetative structures, especially the vascular system, are much more important, systematically, than the external features of non-reproductive parts.

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[1] Throughout this paper the terminations for families, tribes, etc., as recommended by the international congress of botanists at Vienna (1905) and Brussels (1910), have been used, whether or not they have been customarily so used previously.

This principle was clearly recognized and applied, even beyond its legitimate limits, by Seward and Ford when they proposed to separate the Araucarians, on the basis of differences in both these classes of characters, from all other Coniferales, as a separate order, the Araucariales. Chief emphasis was laid on the characters of reproductive structures, but not so much on the gametophytes and embryo, which were then (and are still to a less extent) very imperfectly known, as on the external features and anatomy of reproductive organs. It may be worth while to point out that since the vascular bundles do not, except in rare cases, actually penetrate the reproductive structures, but only those parts of the plant (sporophylls) which bear such structures, the expression "anatomy of reproductive organs" refers to accessory organs, and not to the reproductive structures themselves; consequently such anatomical characters have a systematic value considerably less than characters concerned with the reproductive organs themselves, though somewhat greater than the anatomical characters of purely vegetative parts. Thus, while it was very necessary that attention should be drawn to the fact that the two living genera of Araucarians, which undoubtedly form a small natural alliance, differ in many important respects from all other Conifers, perhaps even more widely than any two other alliances within the group differ from one another, yet it is probable that these differences are of quite the same order as those which may be used to separate other families within the group, e.g. Pinaceæ from Taxaceæ (in the sense in which those families are defined below).

More important, however, than either of the two classes of characters just mentioned are those derived from the internal structure of the reproductive organs. This refers to the ovule, microsporangium, both gametophytes, and, at a later stage, the embryo.

We may sub-divide such characters somewhat as follows:—

1. Structure of young microsporangium.
2. Structure of ovule.

3. Extent of sporogenous ("spongy") tissue in ovule.
4. Sporogenesis.
5. Place of deposition of pollen. (Not logically included in this class of characters, but probably connected phylogenetically with such, and therefore best considered here.)
6. Development and structure of male gametophyte.
7. Early development of female gametophyte.
8. Method of cell formation in female gametophyte.
9. Position of archegonium initials, and of archegonia.
10. Fertilization. (Relative size of male and female nuclei, etc.)
11. Development of pro-embryo, and formation and first divisions of embryo.
12. Later development of embryo. (Number of cotyledons, etc.)
13. Structure and thickness of megaspore membrane.

Of these, numbers 1 and 4, while they are doubtless important characters, show no marked differences, as far as is known, within the Coniferales, and may therefore be left out of account. Numbers 2 and 3 also show only minor differences, except in one or two special cases, where such differences merely serve to emphasize more important divergences in other respects.

Place of deposition of pollen. In the very large majority of Conifers the pollen is deposited on the apex of the nucellus, though occasionally it may be caught before reaching the base of the micropyle, as is said to be normally the case in *Pseudotsuga*, where a constriction half way down the micropyle partially divides it into two chambers, the pollen being retained in the upper. In this genus also the pollen appears to be carried into the upper chamber by an inward folding of the apex of the integument, which develops a special stigmatic surface. Such specialization, while of great interest as being unique among gymnosperms, is probably of much less phylogenetic importance than the "protosiphonogamic" pollination described by Thomson in *Araucaria*, and lately found to be also characteristic of *Agathis*. Here the pollen is deposited on the cone scale or ligule or in the axil of the cone scale, and not, as a rule, on the ovule at all; according to Thomson it may be as much as 3 cm. from the nucellus in *Araucaria*, though it is somewhat surprising to learn that the whole length of the scale is as much as 3 cm. at the time of pollination. At that time the ovule is scarcely differentiated, and there is never a micropylar tube, as there is in most Conifers, the nucellus projecting beyond the end of the integument. In *Saxegothæa* also, the nucellus projects in a similar manner, but in this genus the pollen is deposited on the projecting tip of the nucellus, and not on the scale; thus *Saxegothæa* forms a connecting link between the Araucarians and other Conifers in this respect.

Development and structure of male gametophyte. This is undoubtedly one of the most important guides to the larger relationships. Neglecting minor variations, six main lines of development may be distinguished, which are as follows:—(I) Two prothallial cells formed which persist and proliferate, forming eventually a considerable (but variable) number of free nuclei in the pollen tube; tube nucleus and stalk cell formed (as they are in all cases), and body cell divides to form two nearly equal male cells. Occurs in *Agathis* and *Araucaria*. (II) As I, but body cell nucleus divides very unequally forming one male cell and a much smaller second nucleus lying at its periphery, or sometimes the body cell divides to form two very unequal male cells. (The prothallial cells may persist without dividing in some cases, or one only may persist, as in *Phyllocladus*). Occurs in *Podocarpus*, and some other genera. (III) Two transient prothallial cells formed, then tube nucleus and stalk cell, as usual, and body cell finally divides to form two subequal male cells, or sometimes male nuclei in a common mass of protoplasm. Occurs in *Pinus*, and several other genera. (IV) No prothallial cells formed. Tube nucleus and stalk cell cut off as usual; body cell nucleus divides to form two very slightly unequal male nuclei, which lie free in the cytoplasm of the tube. Occurs in *Sciadopitys*. (V a). As IV, but body cell divides very unequally to form either two very unequal male cells (*Torreya*), or to form one male cell and a second small male nucleus, which lies at the periphery of the male cell (*Taxus*). (V b). As V a, but body cell nucleus forms two equal or nearly equal male nuclei, which are either associated with unequal masses of cytoplasm (thus forming unequal male cells) or are embedded in a common mass of cytoplasm. Occurs in *Cephalotaxus*.

Female gametophyte. As regards numbers 7 and 8, the differences found are either more or less correlated with more important divergences in the position of archegonia, or appear unimportant, as shown by the fact that the method of cell formation is markedly different in the two species of *Sequoia*, which, on other grounds, appear to be very closely related.

The *position of archegonium initials* (number 9) would appear at first sight to be identical with that of mature archegonia, but in two respects this is not necessarily the case, *i.e.*, (i) archegonium initials may be deep-seated, but may grow through to the outside of the prothallus (as in *Sequoia sempervirens*) so that the mature archegonium is superficial; (ii) large numbers of archegonium initials may develop, as in *Callitris* and *Actinostrobus*, of which only those in the neighbourhood of the pollen tube nuclei become mature, functional archegonia.

Neglecting these differences, however, which only affect the present problem indirectly (e.g., as showing that the position of the archegonia is not primarily dependent on the position of the pollen tube) we can recognise in the main four types of arrangement of the archegonia in the prothallus. (I) Separate apical archegonia, each with its own jacket cells (where present), as found in *Pinus*, *Sciadopitys*, *Taxus*, *Podocarpus*, and many other genera. (II) Separate archegonia each with its own jacket cells (where present) but not confined to the apex, as found in *Araucaria* and *Agathis*. (III) A group of apical archegonia, not separated from one another by jacket cells, but usually surrounded by a common layer of such cells, as in *Juniperus*, *Cryptomeria*, *Taxodium*, *Tetraclinis*, and several other genera; in *Cunninghamia* a minor difference is met with, in the occurrence of a group of vegetative prothallial cells in the centre of the archegonial complex. (IV) One or (almost invariably) more lateral groups of archegonia, the individual archegonia not separated from one another by jacket cells as a rule, but the groups often surrounded by a common layer of such cells; occurs in *Sequoia*, *Widdringtonia*, *Callitris* and *Actinostrobus*.

As regards *fertilization* (number 10), there are three grades of size relation between the male and female nuclei (I) In *Araucaria*, *Agathis*, *Sequoia*, *Widdringtonia*, *Callitris* and *Actinostrobus* the two nuclei are equal (or almost equal) in size. (II) In *Pinus* and *Sciadopitys* and several other genera usually associated with *Pinus* there is a very marked difference of size, the female nucleus being many times as large as the male. (III) In all other investigated genera there is a moderate difference in size, the volume ratio between male and female being about 1 : 3 or 4. In connection with fertilization it may be remarked that where an archegonial complex is found, the two male elements are invariably equal, and both are normally functional. Such characters are therefore evidently correlated with one another, and will not be further considered separately.

The *development and structure of the pro-embryo and early embryo* must, in the writer's opinion, be regarded as of primary importance; in this respect, and neglecting minor variations, the following nine types may be distinguished.

(I) A very considerable number of free nuclei (32 or more) are formed in a central mass of cytoplasm in the archegonium ; these are then organised into three tiers of cells, of which the upper forms suspensors, the middle the embryo, and the lowest a penetrating and protective cap. The pro-embryo fills or nearly fills the archegonium. Occurs in *Agathis*, and, with reasonable certainty, though the details are not known, in *Araucaria*.

(II) Walls are laid down during and following the transition from the four-nucleate to the eight-nucleate stage, preceded by the passage of four free nuclei to the base of the archegonium, the first two sporophyte divisions taking place at or near the centre of the archegonium. Subsequent divisions result in the formation of an upper tier of four free nuclei, and three tiers of four cells each below, known as rosette, suspensor and embryo tiers respectively. The pro-embryo only occupies a small part of the archegonium, at its base. This type, which is very constant and regular, occurs in *Pinus* and several related genera.

(III) The type met with in *Sciadopitys* is similar to II, but differs in two particulars—*(a)* that the walls are formed at a later stage, and *(b)* that the embryo cells of the terminal tier divide to form a considerable group of cells (about 16) before the elongation of the suspensors, some of the cells of the group forming a " secondary suspensor."

(IV) In the next type the fusion nucleus before or during, or occasionally just after, its first division, travels to the base of the archegonium and there forms a tetrad of free nuclei (the passage to the base of the archegonium may occasionally be delayed till the four-nucleate stage); wall formation occurs as in type II at the transition from the four- to the eight-nucleate stage, but in this case only three "tiers" (or regions) of cells are usually formed ; nor is the arrangement of cells by any means so constant as in type II ; the number of cells in different tiers may be quite different, and may also vary from one individual to another in the same species, as does also the number of different planes in which the pro-embryo cells are arranged, the cells of one "tier" being not always, in fact rather seldom, in one plane ; it is customary, though not universal, for one embryo cell to be in advance of the others at the extreme base of the archegonium. Although so much variation exists, there is no doubt that this is really a definite type of pro-embryo, and not merely a series of transitional forms between other types ; to convince oneself of this it is only necessary to compare a considerable number of the published figures of different genera conforming to this type, which is common to *Juniperus*, *Thuja*, *Libocedrus*, *Taxodium*, *Cryptomeria*, *Cunninghamia*, *Tetraclinis*, and probably other genera.

(V) In *Podocarpus* and its allies the records are very meagre, but, such as they are, suggest a type where wall formation occurs later than the eight-nucleate stage; where three tiers are normally found in the completed pro-embryo; and where a much larger number of cells is found in the two upper tiers than in the embryo forming tier, which consists usually of only a single binucleate cell.

(VI) In *Torreya* and *Taxus* the pro-embryo nearly or entirely *(Torreya)* fills the archegonium, in contrast to the previous types (except type I) though the number of free nuclear divisions differs widely, walls being formed in the four-nucleate stage in *Torreya*, but not till the 16-32-nucleate stage in *Taxus*. As in type V, the embryo tier consists of only a single cell, but this is uninucleate, not binucleate; as far as our knowledge extends this type does not differ in any other important respect from type V but is more variable.

(VII) *Cephalotaxus* differs from type VI in forming four regions of cells, of which the upper three correspond to those of types IV to VI, while the terminal tier forms a penetrating and protective cap similar to that met with in type I; a somewhat similar phenomenon also appears in a species of *Podocarpus*.

(VIII) The pro-embryo of *Sequoia* differs markedly from that of all other Conifers; there is no free nuclear stage, a wall being formed at the first sporophytic mitosis; the mature pro-embryo completely fills the archegonium, and consists of a row of five large cells, of which the basal forms the embryo, and that next above it the suspensor.

(IX) There is one other type in which the pro-embryo completely fills the archegonium, and which also agrees with *Torreya* (type VI) in the fact that walls are formed at the four-nucleate stage. After some further divisions groups of two or three cells separate out, and in each group the lowest cell forms the embryo and that next above it the suspensor. In this case, as in type VIII, the first two division walls in the embryo initial are vertical. This type is characteristic of *Actinostrobus*, and of *Callitris* as far as is known, while *Widdringtonia* differs from the other two genera in minor points, but agrees sufficiently to be included in the same type.

In the *mature embryo* the number of cotyledons may be a character of some value, but as it varies considerably within a single species it does not appear to be particularly reliable, and will not be further considered.

As regards the *megaspore membrane*, only one investigator (Thomson) has made a comparative study of that structure throughout the Conifers; his results chiefly emphasized the fact that the Araucarians are not very nearly related to any other Conifers.

It will thus be seen that an analysis of a number of characters concerned with embedded reproductive structures reveals the fact that only three of these (structure of male gametophyte, position of archegonia in prothallus, and structure of the pro-embryo) have a sufficient number of distinctive types to be used advantageously in the classification of the group.

The relative value of various anatomical characters has not been discussed here; anatomical characters as a whole are held (for reasons stated above) to be of inferior importance to characters concerned with embedded parts of reproductive structures, and moreover it appears as though there were but little agreement amongst the various students of Conifer anatomy as to the bearing of the known facts on questions of phylogeny and classification. It will however be readily conceded that such important points as the multiseriate pitting of Araucarian metaxylem tracheids, and the combined pitting and spiral thickening in Taxad metaxylem, cannot be overlooked in any scheme of classification; there is even less danger that the claims of external characters of the reproductive organs to be used for classificatory purposes will not be recognised. Consequently, in using the characters which have been discussed as the sole basis of classification, there is no intention to entirely disregard anatomical and external reproductive characters; on the contrary, it will be found that these confirm, as a rule, the evidence furnished by gametophytes and pro-embryo.

III.—VARIOUS SCHEMES OF CLASSIFICATION OF CONIFERS.

As long ago as 1872 Strasburger published a scheme of classification of Conifers in which *Sequoia* and *Sciadopitys* were made the types of two tribes (the second monotypic) ranking equally with the Abieteæ. In the third of his series of Gymnosperm studies in 1900, Arnoldi (as far as one can judge, independently) again proposed to separate *Sequoia* and *Sciadopitys* as the types of two independent tribes, both monotypic in his scheme. It is perhaps curious that both these proposals were made before the facts which completely justify such a suggestion were fully known, but it cannot be too strongly urged, in the opinion of the writer, that there can no longer be any doubt whatever of the correctness of the view that both these genera must be separated in this way. On this view

Sciadopitys becomes an important link between the Abietoïdeæ and the Cupressoïdeæ (in the sense in which those sub-families are defined below), while it simply constitutes an insoluble problem when associated with *Taxodium*, *Sequoia* and other genera, as has usually been the case. Phylogenetically *Sequoia* still remains something of a problem, but one of which possible solutions can be quite reasonably suggested when it is realised that the position of the genus is an isolated one.

Whether these two genera are made the types of a tribe or of a sub-family is of very small importance, and is perhaps not much more than a convention, but it has seemed to the writer most in accordance with our present knowledge of these genera to regard them as the representatives of sub-families; the chief reason for this view is that the differences between each and its nearest allies are of very much the same order as those between the families, while to consider them as tribes only, implies differences of a different, and lesser, order than those used to delimit the families. The only other sub-family, not generally recognised, which the writer considers should be distinct is the Callitroïdeæ, including *Widdringtonia*, *Callitris* and *Actinostrobus*; the claims of this alliance to tribal distinction have been repeatedly urged by the writer, and the only alteration now suggested is to raise the rank to that of a sub-family, on precisely the same grounds as in the case of *Sequoia* and *Sciadopitys*.

It has been assumed in almost every publication dealing with the classification of the Conifers, that within the Coniferales two main families are met with, and two only; but a study of the various schemes reveals the surprising fact that these two families are made up by combining the various tribes in almost every conceivable way. Thus Strasburger, whose view has probably come to be regarded as the orthodox one in this respect, combines Taxads[1] and Podocarps as Taxaceæ, and the rest of the Conifers as Araucariaceæ. Essentially the same arrangement, though often with different names, has been followed by Eichler in Germany, by Coulter and Chamberlain in America, and by Masters in England. Beissner includes Podocarps (exclusive of *Phyllocladus*), Araucarians (including *Cunninghamia* and *Sciadopitys*), and Abieteæ in one "Series"; Cupresseæ, Taxodieæ and Taxeæ in another. Hansen, a year later, followed Beissner's grouping exactly, while very recently Stiles has argued in favour of Beissner's scheme, though his tribes are differently limited in some respects. Tison has upheld the view that the Araucarians, *Saxegothæa* (regarded by him as intermediate between Araucarians and Podocarps) and the other Podocarps should constitute one series, as against all the other Conifers. Seward has advocated separating the Araucarians alone from all other Coniferales, as a separate order the Araucariales. Lotsy has recently proposed to associate Araucarians (including *Cunninghamia*), Podocarps (including *Phyllocladus*) and Cupresseæ (as usually understood) in one family; Taxads, the old Taxodieæ, and Abieteæ in another.

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[1] This, as in all the older classifications includes *Ginkgo*, now generally recognised to belong to a quite different phylum.

The latest classification is that of Vierhapper, but in this case it is definitely stated that no account is taken of gametophyte structures. He, like all the rest, has two families, "Taxocupressaceæ," including three sub-families, Taxoïdeæ (Taxads and Podocarps), Taxodioïdeæ, and Cupressoïdeæ; and "Abietaceæ," also including three sub-families, Araucarioïdeæ (*Agathis* and *Araucaria*), Cunninghamioïdeæ (*Cunninghamia* and *Sciadopitys*) and Abietoïdeæ (as usual). These sub-families are further classified into tribes and sub-tribes, the latter often including only a single genus.

The only exception I have noted to the two-family schemes of classification is the arrangement by Wettstein, who has three families sub-divided as follows:—

I.—Taxaceæ.
  i. Cephalotaxeæ. (*Cephalotaxus*).
  ii. Taxeæ. (*Torreya*, *Taxus*).
  iii. Podocarpeæ. (As usual, including *Phyllocladus*).
II.—Cupressaceæ.
  A. Taxodioideæ. *Arthrotaxis*, *Sequoia*, *Cryptomeria*, *Taxodium*).
  B. Cupressoideæ. (As usually understood).
III.—Abietaceæ.
  i. Araucarieæ. (*Agathis*, *Araucaria*).
  ii. Cunninghamieæ. (*Cunninghamia*, *Sciadopitys*.)
  iii. Abieteæ. (As usual).

Wettstein has been followed by Porsch, though apparently only in regard to the three families, and not in all the sub-divisions. The separation of Cupressaceæ from Abietaceæ is undoubtedly justified, but apart from this Wettstein's grouping shows no advance on previous arrangements.

That *Cephalotaxus* is the most primitive genus of *Taxoïdeæ*, as maintained by Porsch, is in accordance with the views here put forward in regard to Taxad phylogeny, but the resemblances to

Ginkgo are probably almost wholly due to convergence, and cannot be held to indicate any near relationship between Taxaceæ and Ginkgoales.

IV.—CLASSIFICATION OF CONIFERALES NOW PROPOSED.

These examples (which do not include all the arrangements that have been proposed) amply substantiate the statement that the smaller alliances have been grouped in almost every possible way by different investigators.

To the writer each of these systems appears unsatisfactory; it would rather appear that five families must be recognized, which, according to the character regarded as of paramount importance, may be combined in several different ways, as indicated in these various schemes; when the sum of these characters is taken into consideration, each such grouping is found to break down.

These five families are therefore regarded as having approximately equal rank within the Coniferales. They are:—I. Araucariaceæ (*Araucaria* and *Agathis*); II. Podocarpaceæ (*Podocarpus*, *Dacrydium*, *Microcachrys*, *Saxegothæa*, *Phyllocladus*, and probably *Pherosphæra*; III. Pinaceæ (with two sub-families defined below); IV. Cupressaceæ (with three sub-families defined below); and V. Taxaceæ (*Taxus*, *Torreya*, *Cephalotaxus*, and possibly *Acmopyle* and *Polypodiopsis*). Of the genera mentioned, *Phyllocladus* was at one time regarded as a connecting link between Podocarps and Taxads, but nearly all modern investigators are agreed that it is clearly related far more nearly with the Podocarps (see Coulter and Chamberlain's *Morphology of Gymnosperms* for a concise summary of the evidence on this point), while a very strong case for the wide separation of Podocarps from Taxads has recently been ably put forward by Stiles. The two suggested sub-families of the Pinaceæ, with the genera included in each of them, are as follows:—

i. Abietoïdeæ (*Pinus*, *Larix*, *Pseudolarix*, *Picea*, *Tsuga*, *Pseudotsuga*, *Abies*, and probably also *Cedrus* and *Keteleeria*).
ii. Sciadopitoïdeæ (*Sciadopitys*).

and the three of Cupressaceæ are:—

i. Cupressoïdeæ (*Thuja*, *Libocedrus*, *Juniperus*, *Tetraclinis*, *Taxodium*, *Cryptomeria*, *Cunninghamia*, and probably *Cupressus*, *Biota*, *Chamæcyparis* and *Thujopsis*, and possibly also *Glyptostrobus*, *Taiwania* and *Athrotaxis*).
ii. Callitroïdeæ (*Widdringtonia*, *Callitris*, *Actinostrobus*, and possibly also *Fitzroya*).
iii. Sequoïdeæ (*Sequoia*).

The position of certain genera in this scheme of classification is quite uncertain, as has been indicated. Those included under the heading of "probably" in the families and sub-families are not considered likely to show marked divergences in gametophyte and pro-embryo characters, when these are more fully known, but the position of those "possibly" included is very uncertain, and the genera *Fitzroya* (including *Diselma*), *Athrotaxis*, *Glyptostrobus*, *Taiwania*, *Acmopyle*, *Polypodiopsis* and *Pherosphæra* would certainly repay a detailed investigation. If, however, the general principles used as the basis of such a classification are regarded as valid, it cannot be logically urged that some other and more artificial grouping of the genera should be preferred, which would enable every genus to be at once placed in its final position. On the contrary, the uncertainty in regard to the natural position of these genera can only be used as an argument for their immediate investigation. A more serious disadvantage is that we have an extremely limited acquaintance with gametophyte and pro-embryo structures amongst fossil Gymnosperms; still, the same argument applies, that we cannot discard a natural in favour of an artificial classification for the sake of cataloguing fossils, though there has been a tendency of late to do something of this kind.

The families and sub-families here proposed may be defined (in regard to gametophyte and pro-embryo characters only) as follows:

I. Archegonia more or less lateral, not united in groups; apex of prothallus truncate; male gametophyte with a considerable number of prothallial nuclei; male cells nearly equal; pro-embryo forming a considerable number (32 or more) of free nuclei in a central mass of cytoplasm, before wall-formation; lowest tier of cells forming a penetrating and protective cap; male and female nuclei equal (or almost equal) in size at the time of fertilization. - - - - - - - *Araucariaceæ.*

II. Archegonia apical, each with its own jacket-layer, not united in a complex; male gametophyte with two or more prothallial nuclei, usually persistent; male cells very unequal; pro-embryo forming about 16 free nuclei before wall-formation, at base of archegonium; usually no cap-cells; single binucleate embryo-cell at the tip of the pro-embryo. - - - - *Podocarpaceæ.*

III. Archegonia as in II; male gametophyte with two transient prothallial cells, or none; male cells (or nuclei) nearly equal; pro-embryo with eight or more free nuclei at base of archegonium before wall-formation, later organising four regular tiers of cells (free nuclei, rosette, suspensor and embryo tiers); male and female nuclei very unequal in size at the time of fertilization. - *Pinaceæ.*

III. i. Archegonia as in family; male gametophyte with two prothallial cells, not persistent; male cells nearly equal; pro-embryo forming eight free nuclei at base of archegonium, before wall-formation; four tiers of (*a*) four free nuclei, (*b*) four rosette cells, (*c*) four suspensor cells, and (*d*) four embryo-cells *Pinaceæ*: *Abietoïdeæ.*

III. ii. Archegonia as in family; male gametophyte with no prothallial cells; two nearly equal male nuclei lying free in the tube cytoplasm; pro-embryo forming more than eight free nuclei at base of archegonium; four tiers formed as in III. i. but terminal tier dividing to form a group of about sixteen cells before elongation of the suspensors. - - - - *Pinaceæ*: *Sciadopitoïdeæ.*

IV. Archegonia apical or lateral, more or less united in one or more groups or complexes, with a common jacket-layer (where present); male gametophyte without prothallial cells; male cells exactly equal and clearly defined, at first hemispherical, and both functional as a rule; pro-embryo with not more than eight free nuclei before wall-formation, otherwise differing widely in the three sub-families; male and female nuclei not differing widely in size at the time of fertilization. - - - - - *Cupressaceæ,*

IV. i. Archegonia in a single apical complex, surrounded by a common jacket-layer (in one genus some vegetative cells are included in the centre of the complex); male gametophyte as in family; pro-embryo forming eight free nuclei before wall-formation, occupying only a small part of the archegonium at its base; mature pro-embryo usually of three tiers or regions, less regular in arrangement than in III, commonly with one of the cells of the embryo region in advance of the others; male nucleus distinctly smaller than female at the time of fertilization. - *Cupressaceæ*: *Cupressoïdeæ.*

IV. ii. Archegonia in one or (usually) more lateral groups, each with traces of a common jacket-layer; apex of prothallus pointed; male gametophyte as in family; pro-embryo forming four free nuclei before wall-formation, filling the archegonium, and dividing up into several groups of two or three cells, of which one becomes the suspensor and one the embryo initial; male and female nuclei equal (or almost equal) in size at the time of fertilization. - - - - - *Cupressaceæ*: *Callitroïdeæ.*

IV. iii. Archegonia in several lateral groups; apex of prothallus pointed; male gametophyte as in family; pro-embryo becoming walled at first division; mature pro-embryo filling the archegonium, and consisting of about five cells, of which the basal forms the embryo initial, and the next the suspensor; male and female nuclei equal in size at the time of fertilization. - - - - - - *Cupressaceæ: Sequoïdeæ.*

V. Archegonia as in II and III; male gametophyte without prothallial cells; male cells very unequal; pro-embryo somewhat variable, forming from four to thirty-two free nuclei before wall-formation, nearly or quite filling the archegonium; in one genus the terminal tier forms a protective cap, as in Araucariaceæ, otherwise the mature pro-embryo is similar to that of Podocarpaceæ, with the exception that the single embryo initial is uninucleate, not binucleate. - - - - - - - - *Taxaceæ.*

V.—PHYLOGENY OF CONIFERALES.

While the present state of our knowledge of the Coniferales seems to lead quite naturally to a classification more or less on the lines here suggested, there is much greater difficulty in trying to fit the known characters of the genera into any satisfactory scheme of phylogeny. It may be taken as a starting point that the Conifers are monophyletic, an opinion evidently held by the very large majority of the recent workers on the group. Each of the families is clearly related, either directly or through a third family, with each of the others. Thus the male gametophyte of Araucariaceæ, Podocarpaceæ and Abietoïdeæ indicates a common ancestry for the first three families; the archegonia and pro-embryo of Podocarpaceæ and Taxaceæ indicates for these two a common, though perhaps more remote, origin; while *Sciadopitys* is clearly a connecting link between Abietoïdeæ on the one hand and Cupressoïdeæ on the other (though much more nearly related to the former), thus connecting the Cupressaceæ with the Pinaceæ.

To the writer it seems altogether inconceivable that any of the Gymnosperms can have been derived from Lycopod ancestors. Both gametophytes in the Cycads, Ginkgo, and the Coniferales point to the conclusion that these three phyla originated from the same plexus, and, thanks to recent palæobotanical research, there is every reason for believing that this plexus was fern-like in origin, and not derived from the palæozoic Lycopods. As far as the Cycads are concerned, such a view appears to have been quite definitely accepted, and on the whole the case for the derivation of Conifers and Ginkgoales, through or near the Cordaitales, from a similar origin, seems equally strong.

The best case for the opposite view has recently been stated by Mr. Stiles, his chief argument against the Cordaitalean origin being that, because the Podocarps differ rather widely from the

Cordaitales, and are considered (no doubt rightly) to be related to the Araucarians, therefore the Araucarians cannot be also related to the Cordaitales. The simple explanation would appear to be that the Araucarians are more primitive than the Podocarps, and that the latter have advanced further from the ancestral Cordaitalean type than the former.

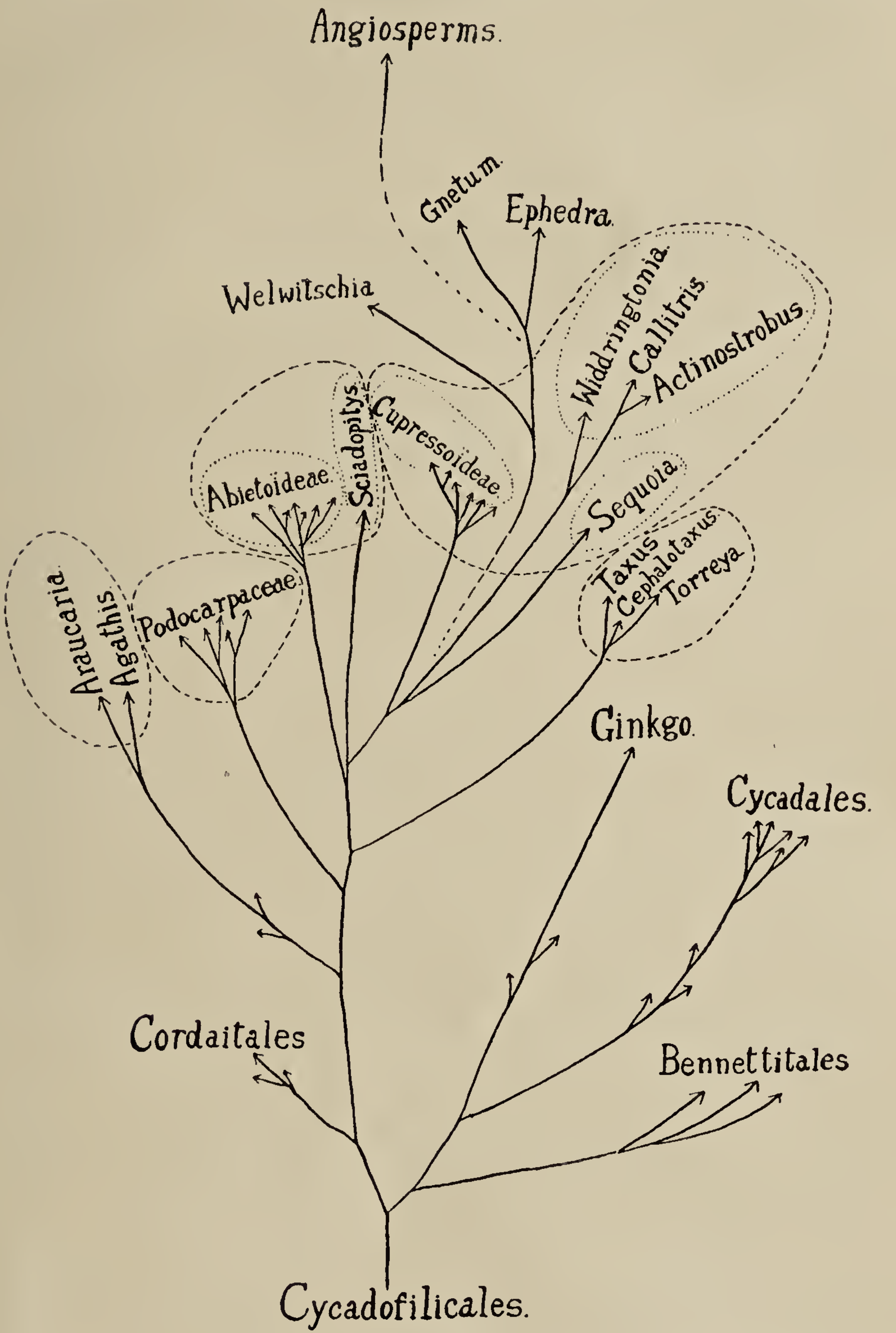

Fig. 1. Suggested scheme of the Phylogeny of Gymnosperms.

It is not possible to indicate fully the various divergences, convergences and relationships of any phylum in a diagram confined to two dimensions, but a general idea of Gymnosperm phylogeny according to the views here put forward is given in the accompanying chart.[1] It must, however, be admitted that the data are at present insufficient to establish the true sequence of Gymnosperm phylogeny with any certainty.

For the sake of simplicity, and to avoid repeated duplication of numerous references, the sources of information have not been individually acknowledged in the preceding account. These sources are, however, given in the following list of references; the list is by no means intended to be a complete bibliography of Conifer literature, but an attempt has been made to include all the important sources of information and opinion, in regard to the immediate subject of the essay; references to purely anatomical work have not, as a rule, been included.

It may be added that a discussion of this kind could be almost indefinitely lengthened if all the minor characters which may be used in certain cases for purposes of sub-division were taken into account; such characters have been often purposely passed over for the sake of brevity, and in order not to obscure the main question. For a similar reason sub-division has not been carried further than the families and sub-families; opinions have differed far less as to the smaller sub-divisions, than in regard to the main outlines of classification, and there seems no objection to the continued use of the smaller groups of genera, limited as at present; in the opinion of the writer, however, there is at present no justification for grouping together those genera of the Cupressoïdeæ (as here defined) formerly united in the tribe Taxodieæ, in any sub-division of a higher order than a sub-tribe, and even this seems unnecessary; the Cupressoïdeæ form a very well defined sub-family, and, the number of genera being fairly small, it is not necessary for purposes of convenience to group them into smaller alliances of an artificial character.

In conclusion the writer wishes to express his thanks to Professor H. H. W. Pearson, and to Professor A. C. Seward, for criticism in regard to certain points.

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[1] Gymnosperms other than Conifers are included in the Chart, but are arranged more or less in accordance with widely accepted views, as put forward—*e.g.*, in Coulter & Chamberlain's *Morphology of Gymnosperms*.

Botany School,
Cambridge.
June, 1913.

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REVIEW.

BRITISH HEPATICS.

FOR many years the students of these plants have felt the need of a work to give them further information and a better means of identification than could be obtained from the works of Cooke, Carrington, and Lett. This want was, to some extent, supplied by Pearson's "Hepaticæ" (1) but the cost of this work was beyond the reach of many bryologists, and there was still plenty of room for a Manual at a less price and of a similar character to Dixon's handbook on the mosses (2). Hepaticologists can now rejoice in being able to possess such a work (3) and must feel deeply grateful to its author for the careful attention he must have devoted to the subject, in order to produce such an excellent handbook, remarkable not only for its lucid descriptions and notes, but also for its scientific accuracy, a combination not always obtained from systematists.

The introduction gives a short and general account of the life-history of a liverwort, with some excellent notes on the collection and examination of specimens. The classification is based on Schiffner, many of the descriptions of the higher groups being taken directly from the works of this distinguished hepaticologist, but the author has not neglected the works of Campbell, Evans, Howe, Müller, Spruce, Stephani and Cavers, the recent papers (4) of the latter being responsible for the elevation of the Sphærocarpales to ordinal rank.

More species are given as British than in any previous work, this increase being partly due to recent discoveries and partly the result of segregation. The author can, however, hardly be considered to be a "splitter," neither can he be charged with being a "lumper," *in media re salus*, seems to be an excellent motto in this matter.

Calypogeia, long known to British botanists under the name of Kantia, has seven species assigned to it, five others besides the distinct *C. Trichomanis* and *C. arguta* taking specific rank. The three larger species, *Trichomanis*, *Neesiana* and *fissa* (*Kantia Sprengelii*, Pears.) are chiefly distinguished by the underleaves, which often vary in the same plant, and great difficulty is often experienced in deciding which of these names a specimen should bear, so that, at most, they can only be considered as "small species." *C. sphagnicola*, *submersa*, and *suecica* must be treated similarly, their specific distinctions from small forms of *C. Trichomanis* being of a more or less doubtful nature. A variety *aquatica* is given for *C. Trichomanis* whilst the equally definite aquatic form of *C. fissa* is not mentioned.

Plagiochila has six species allotted to it, *P. Stableri*, "although only once collected and in small quantity," being judged as a distinct species. I have found occasional shoots of *P. asplenioides* var. *humilis* with an appearance almost exactly like that figured for *P. Stableri*, and as the original specimen was mixed with some of this variety, it may be a modification induced by edaphic conditions; *P. exigua* is reduced to a habitat-form of *P. tridenticulata*, *P. killarniensis* to a variety of *P. spinulosa*, and *P. Owenii* to a variety of *P. punctata*.

Lophocolea has a fifth species (*L. alata*) granted to it; this scarcely seems more than a variety of *L. cuspidata* with the wings of the perianth more highly developed. The confusion between the two species, *bidentata* and *cuspidata* has been dissolved, and *L. fragans* replaces the better-known name of *L. spicata*.

Cephalozia has fourteen species, nine species formerly placed under this genus being allocated to Cephaloziella; *C. curvifolia* is placed in Nowellia, a genus named after the Yorkshire botanist Nowell; *C. trivialis* and *C. Curnowii* are included in *C. bifida*, and *C. Jackii* in *C. myriantha*, the smallness of these plants and the minuteness of some of the distinguishing characters causing differences of opinion of a quite legitimate nature as to the delimitation of these "small species."

There are six British species of Fossombronia, these being distinguished chiefly by the number of lamellæ or papillæ on the spores; in Riccia there are twelve species, *R. natans*, on account of its structure being placed in the genus Ricciocarpus. The Pallavicinia of most British authors is split up into two genera, Pallavicinia with one species, *P. Lyellii*, and Moerckia with three; *Conocephalum conicum* represents our old friend Fegatella; *Pellia endiviæfolia* (*calycina*) appears in the unfamiliar guise of *P. Fabbroniana*; Nardia is represented by four species respectively of Alicularia and Eucalyx, and Mylia has been displaced by Leptoscyphus. The old genus Lejeunia is separated into six genera, Lejeunea in its more restricted sense having six British species, Cololejeunea four, whilst *Harpalejeunea ovata*, *Colurolejeunea calyptrifolia*, *Drepanolejeunea hamatifolia*, and *Microlejeunea ulicina* have their own generic names. Marchesinia claims priority to Phragmicoma by a single year and Gymnocolea is restored to the generic rank from which it had been temporarily displaced, the common species, *G. inflata*, having as a companion, *G. acutiloba*, of doubtful distinctness to *G. inflata* var. *heterostipa*, which has now found a resting-place from its tossings to-and-fro between Gymnocolea and Cephalozia.

The more definite Jungermannia species are placed under Lophozia, containing twenty-six species, some of which are of doubtful specific value and can only be considered as "small species." *L. turbinata* and *L. badensis* are often difficult to distinguish from each other, the cell-size and amount of thickening ("trigones") at the cell-angles being variable in both plants. The three species, *L. Floerkii*, *L. attenuata* and *L. atlantica*, though quite distinct in their extreme forms, have many intermediates which are difficult to refer to either, as the author subtly says "two allied species vary in parallel lines so that the student may think that they have intergraded when such is not the case." The abundance of moisture causes *atlantica* to approach *Floerkii*; on the other hand, the drier ground form of *Floerkii* has a very similar facies to that of *atlantica*. There is a drier ground form of *L. ventricosa* which bears a somewhat similar relationship to the type as *L. atlantica* does to *L. Floerkii*.

Scapania with twenty-one species still retains the limits usually assigned to it, being practically the only genus, having more than five species, with unaltered boundary.

In some cases (*e.g.*, Aneura and Cephaloziella) great importance is attached to the distribution of the sexual organs, the unisexual or bisexual nature of the plant, being the character deciding its name. It may seem like heresy to the systematic bryologist tc question the importance of this character, but a specific distinction based on such an unsatisfactory foundation is scarcely warrantable, especially when other species are not treated similarly. The paroicous and monoicous conditions of *Calypogeia Trichomanis* are not considered specifically distinct, but a similar sexual distribution in Cephaloziella causes a segregation into two distinct species, other differences being of minor importance in the naming of a doubtful plant. The same uncertainty of specific distinction is shown in *Aneura latifrons* and *A. incurvata*; the former is monoicous, usually broader, more branched and plano-convex in section, whilst the latter is dioicous and concavo-convex in section. The characters separating these two plants are very variable, dioicous plants sometimes having the form and section of *A. latifrons*, in fact, the shape of the cross-section of the thallus may vary in the same specimen, in which case the sexual distribution seems to be the only distinguishing character between the two species. *Cephalozia Lammersiana* was regarded by Spruce as a larger and dioicous form of *C. bicuspidata*, whilst Macvicar considers it to be only "pseudo-dioicous," and as "a 'small species' which is probably not always separable from *C. bicuspidata*." In the nomenclature of mosses (2) the same unsatisfactory distinction occurs, *Bryum bimum*, being synoicous, is separated from *B. pseudo-triquetrum* which is dioicous, the autoicous *B. pallescens* from the synoicous *B. affine*, the distribution of the gametangia being the only constant separating feature. In *B. capillare* the synoicous state is simply given as a variety of the dioicous type, and *B. inclinatum* and *B. provinciale* may be autoicous or synoicous, sometimes both arrangements of the gametangia occuring on the same plant.

There are seven species of Aneura given; those most recently segregated, *A. incurvata* and *A. major*, are probably much commoner than indicated, especially if the simple and concavo-convex character of the thallus be taken as the deciding factors of the former. The *crassior* form of *A. pinguis* found on sand dunes seems to be as worthy of a varietal name as many others which have been accorded that doubtful dignity.

The use of a varietal name is, as the author says, "largely a matter of personal opinion," and probably no two hepaticologists could be found to agree in all cases, but the values of some of the varieties given in the Handbook seem unequal to me. Of doubtful value may be mentioned such varieties as the following, *Riccia glauca* vars. *major*, *minor*, *subinermis*; *R. bifurca* var. *subinermis*; *R. Warnstorfii* var. *subinermis*; *Scapania gracilis* var. *minor*; *Chandonanthus setiformis* var. *alpinus*; *Lophozia Floerkii* var. *Naumanniana*; *Alicularia scalaris* var. *procerior*; and *Cephalozia media* var. *laxa*. In most cases these are growth-forms due to habitat, as such a good ecologist as Macvicar no doubt recognises. The erect, truly aquatic form of *Pellia Fabbroniana* is given as var. *lorea*, the similar habitat-form of *Marchantia polymorpha* is var. *aquatica*, the more xerophytic and alpine form of the latter being distinguished as var. *alpina*.

Alicularia Geoscyphus has a form of shady or moist ground which is the var. *suberecta* (=*Jungermannia silverettæ*); in intermediate habitats all stages between the type and the variety can be found and "it cannot always be distinguished from the typical plant" (3).

No varieties are given for *Gymnocolea inflata*, but from the way in which varietal names have been bestowed, some of its forms have a right to be classed as varieties, since a great difference exists between the two extremes, the form *compacta* of dry situations, and the form *natans* which occurs as free-swimming tufts in pools.

Lepidozia pinnata has a var. *minor*, whilst the equally distinct laxer state is merely referred to as form *laxa*, the lax form of *Lophozia Schultzii* being styled var. *laxa*. The confusion between the greenish, less-toothed forms of *Scapania dentata* (more familiar as *S. purpurasceus*) and the purplish, more or less toothed forms of *S. undulata* is avoided by placing the "intermediates" in the var. *ambigua* of the former, a procedure which is certainly warranted by my experience of the plants, though it leaves some room for doubt as to the specific distinction between *undulata* and *dentata*. The larger-celled form of *Chiloscyphus polyanthus*, which has been so often mistaken for *C. pallescens* is called var. *fragilis*.

These criticisms are not in any sense, to be taken as pointing out defects in the work, but as indicating the different points of view that may be considered by other hepaticologists in using specific and varietal names. Mr. Macvicar is too good an ecologist to be dictatorial in such matters, and many of the names used have doubtless been adopted after some hesitation, and in some cases he may have sunk his own personal opinion below that of other writers.

It is extremely interesting to note, that owing to the aid and stimulus which this work has given to British students since its publication, seven species and one variety have been added to our Hepatic flora, and that most of these were mentioned in the attractive foot-notes as likely to occur in our isles. *Marsupella apiculata*, *Lophozia longiflora* and *Diplophyllum gymnostophilum* have been found in the Scottish Highlands, *Lophozia confertifolia* in N. Ireland and Sussex, *Cephaloziella Douini* in Kent, *C. pulchella* in Northants and Yorkshire, and *Riccia commutata* and its variety *acrotricha* in Sussex. This is a striking testimony to the value of the work, which gives not only descriptive notes and excellent keys of the genera and species, but is also well-indexed and ably illustrated by W. G. Jameson, to whom, as well as to the author, the British students of these plants feel a deep debt of gratitude.

W. WATSON.

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(2). Dixon, H. N. "The Student's Handbook of British Mosses." Ed. 2, London, 1904.

(3). Macvicar, S. M. "The Student's Handbook of British Hepatics." London, 1912.

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AQUILEGIA VULGARIS DOMINANT.

WHEN we first saw it there was a purple patch on the hillside nearly a quarter of a mile away, not quite the colour of the bluebell, but rather a deeper violet, and rousing our curiosity. Someone climbed and shouted down "columbines," then we all scrambled up, and saw to our amazement a great bed of columbines, as big as a garden, in full flower. I have just been again to see them in flower this year, on May 28th, and to examine rather more carefully the conditions of their growth. The valley below is a shimmer of blues, fading bluebell and full-flowered forget-me-not. A few globe flowers are opening near the clear tinkling stream. But these columbines are perched high on the side of the valley nearly 500 feet above sea-level. The valley winds a little, here the steep bank faces nearly S.W. The ground is very stony, geologically oolite; three sample pebbles which I took home with me all effervesced with acid. No streams run down the slopes, for the oolite is a very porous rock. The ground has recently been cleared of timber, and a few oak stumps are sprouting again. The general character of the adjacent country is fairly represented in J. Walter West's picture of "Timber Cutting in North Yorkshire." Here replanting has been done with larch. Other parts of the bank are green with new bracken or white with garlic. The patch of columbine is curiously compact, in shape roughly oval, the longest axis about thirty yards. There are few stragglers from the main body, few plants are more than one yard from their nearest neighbours, just one outlier was some six yards away. Where the plants were densest they were perhaps sending up sixty flowering stalks to the square yard, which would mean say a dozen plants.

Here their leaves were so close as not quite to carpet the ground, yet one could not step without crushing them. Other plants which grew in and out among them were dog's mercury, a bramble, a grass, woodruff, strawberry, sanicle, a ragwort, herb Robert, dandelion, garlic. Some other parts of the bank seemed a little drier, and there some thistles were growing. At the date named (May 28th) the leading flowers on the taller and older plants were well opened, some younger plants with single flower-stalks had no flowers opened. It was dull, 11 a.m., and a few raindrops were falling. A few bumble-bees (body-colour black, white and yellow) were at work, probing the flowers from below. The well-grown plants were mostly about 2 feet 6 inches high; if I were writing a florist's catalogue I could say 3 feet for a few of them without being absolutely untruthful. The flowers were blue purple in colour, except for six plants with white flowers near the densest part of the patch. There are no cattle grazing on the bank. Wire-netting seems to exclude rabbits.

The "wild" columbine is generally regarded as a garden escape, but in these valleys it is admittedly native. The circumstances detailed above suggest that the patch may have originated from a much smaller group or even a single plant, and that in some way the clearing of the ground has favoured them. I saw no columbines elsewhere in the woods that day, which rather suggests that the growth of overhead shade will discourage them in future years. Their present dominance on a restricted area suggests very favourable conditions for just the last few years. The sharp boundary of the patch suggests that even when the wind shakes the ripe follicles the seeds cannot be flung for more than a few yards.

Bootham School, York. HUGH RICHARDSON.
May, 1913.

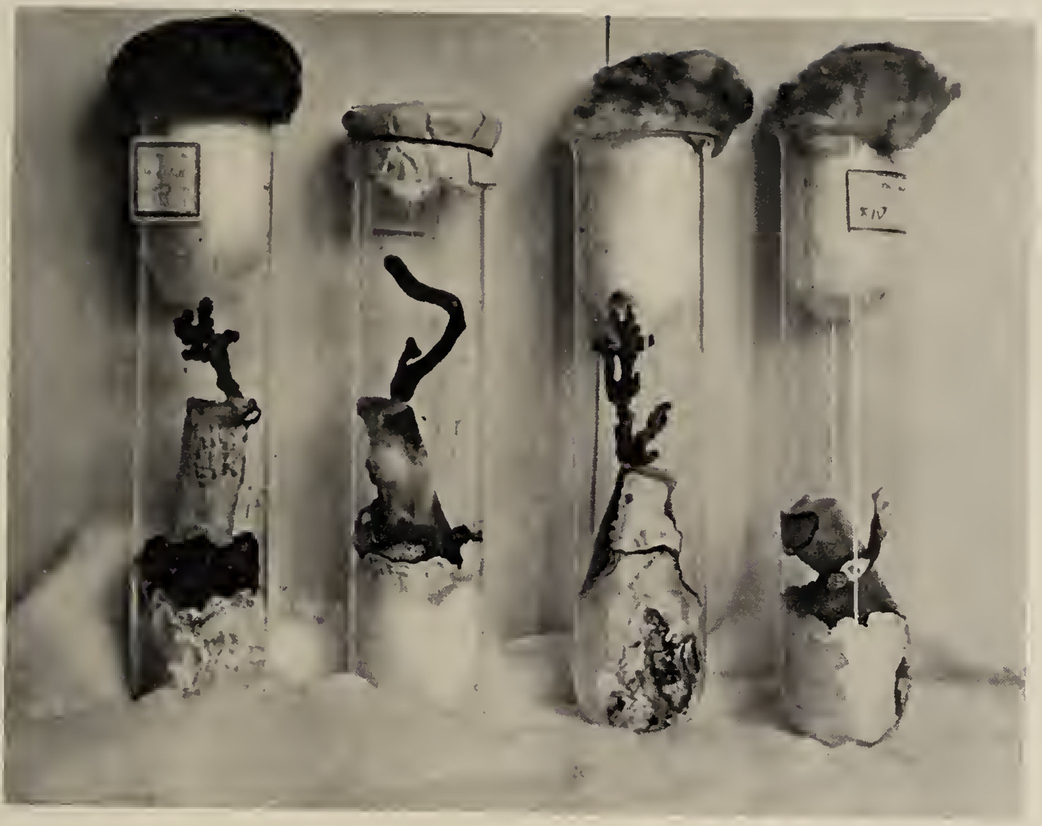

Fig. 1.

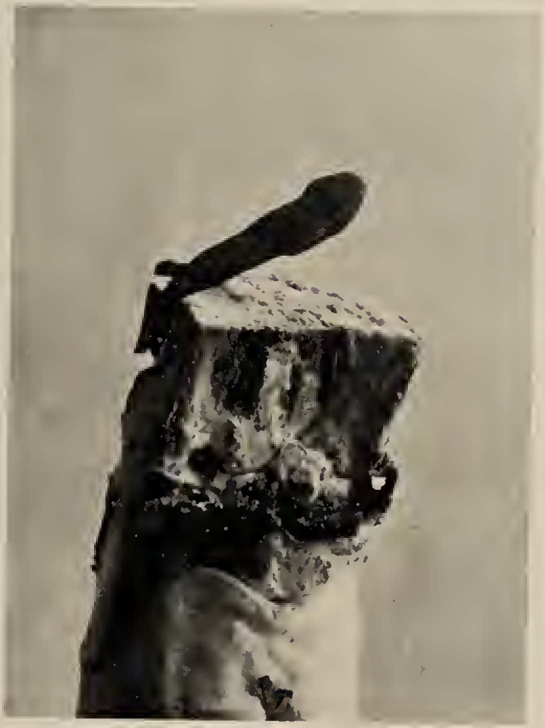

Fig. 2.

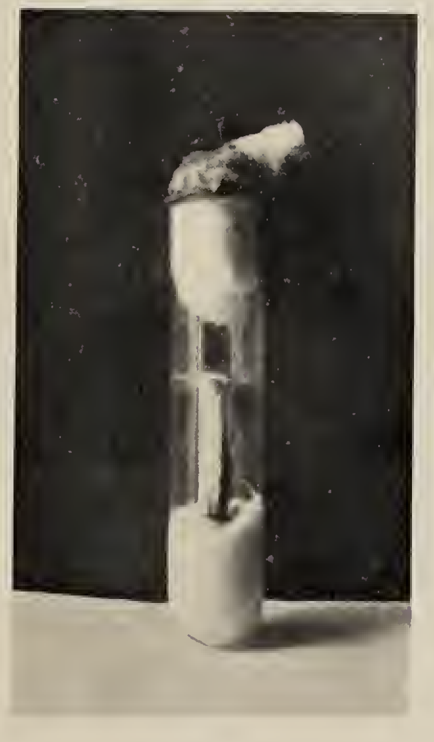

Fig. 3.

PRICE.—POLYPORUS SQUAMOSUS.

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ON *POLYPORUS SQUAMOSUS* HUDS.

BY S. REGINALD PRICE, B.A.,
Frank Smart Student in Botany in the University and
Late Scholar of Clare College, Cambridge.

[WITH PLATE VI AND FOUR FIGURES IN THE TEXT].

INTRODUCTION.

POLYPORUS SQUAMOSUS Huds., known popularly as the "Great Scaly Polyporus," the "Saddle-back Fungus" (6) or the "Dryad's Saddle" (13, p. 101), is one of the best known of tree-destroying fungi. It is frequent throughout Europe and occurs in America. Although it is probably commonest on the various Elms, it is found on many species of Dicotyledonous trees. No record of it on Conifers is to be found. The fruit bodies are produced from May to September[1] and vary greatly in size. Of the observations which have been made on the biology of this species, the most important are embodied in papers by Buller (6), also in the same author's "Researches on Fungi" (7), and by Mr. F. T. Brooks (3).

The Present Observations. It was suggested to me by Mr. F. T. Brooks that certain points in the biology of *Polyporus squamosus* required investigation, especially with regard to the methods of infection in nature and to the destruction of wood in pure culture. A few cultures obtained by him in the summer of 1911, by placing fresh spores on the surfaces of sterilised Elm wood blocks, were handed over to me. The results of these investigations are here described. The fungus has not previously been grown in pure culture on wood blocks (11).

[1] After the wet summer of 1912, followed by a mild autumn, fruit-bodies were found on November 15th at the Botanic Gardens, Cambridge.

I. *POLYPORUS SQUAMOSUS* IN ARTIFICIAL CULTURE.

(*a*). *The establishment of pure cultures on blocks of wood.* Attempts were made to raise further cultures on Elm wood and to follow the development of the mycelium from the spores.

The method employed was generally that used by Marshall Ward (14) for *Stereum hirsutum*, and by Brooks (4) for *Stereum purpureum*.

By making use of the spore-cloud formation of the fructifications as described by previous investigators (3, 6), pure spore-deposits were obtained on sterilised glass slips, the spores being transferred to the blocks by means of a platinum needle.

Up to December 6 there was no sign of any mycelial growth observed on the blocks inoculated with spores on October 23. It was hence concluded that the cultures had failed, so that some were thrown away. When the cultures were next examined, however, on January 17, 1912, a well marked mycelial development was obvious. As the mycelium was similar in all nine cases, and also similar to those begun in August, 1911, it was concluded that this was the mycelium of *P. squamosus*—which, however, took about two months to manifest itself.

Mycelial transfers to other culture tubes grew slowly, a month being required for the growth of a thin layer. The mycelium spread gradually and grew in thickness, till after three or four months a dense white "felt" covering the whole outer surface of the block was produced (Pl. VI, Fig. 2). At about this stage the felt became tinged with a pale brown colour exhibiting at the same time a dusty appearance; this coincided with the production of "oidia." Soon after this stage the mycelium usually began to exude glistening drops of liquid from its surface which were at first colourless, but subsequently assumed a light brown tint, the mycelium also usually becoming darker brown at this stage. The liquid drops increased in size and ran together and often a few cubic centimetres of the liquid collected in the culture tube. Experiments showed that this liquid was water, coloured by some decomposition product. Similar exudations of water by the ripe fruit bodies of *Polyporus* and other fungi often take place (3, p. 350).

Only on Elm wood were spore cultures made. Mycelial transfers were made to the following kinds of wood—Lime, Sycamore, Horse Chestnut and *Pinus*. Copious growth occurred on the wood of Lime, Sycamore and Horse Chestnut, but only a very sparse development of the mycelium took place upon that of *Pinus* (Pl. VI, Fig. 3).

In the case of the Horse Chestnut wood, sterilisation was effected by treatment with hydrogen peroxide, the excess being subsequently removed by treatment with dilute potassium permanganate solution acidified with sulphuric acid. The blocks so treated remained sterile, and no discolouration of the wood took place, while in most cases the mycelium grew fairly readily on those inoculated.

(*b*). *The development of abnormal fructifications.* The first sign of any fructifying bodies appeared on one of the original Elm wood cultures towards the end of April, 1912, about eight months after it was set up. Later many of the other cultures growing in dull light also produced fructifications of a similar type, chiefly in June and July. Thus on August 7, 1912, there were thirteen fructifications, some produced from blocks inoculated on October 23, 1911, and others from blocks inoculated as late as March 5, 1912.

Each fructification arose as a small white or brownish hemispherical excrescence from the general mycelium, often from near the upper end of the block of wood, but in one case from the surface of the cotton wool plug, near the wood, which the mycelium had permeated. Growth proceeded rapidly, but the fructifications produced never took the normal bracket form.

Often they appeared as unbranched structures, of an "Indian club" shape, though only slightly enlarged at the distal end (see Pl. VI, Fig. 2), but some were variously branched, producing peculiar "tree like" growths such as those shown in Pl. VI, Fig. 1. They show a geotropic response, as they assume a more or less vertical direction of growth after first growing out at any angle. As they get older they become dark brown in colour, often only just the tip of the fructification appearing white. These fructifications remained quite sterile, microtome sections cut in various regions failing to show any sign of the formation of a hymenial surface or of basidia.

In general appearance the fructifications are on the whole similar to those described by Buller (7, pp. 57-59) as developed in the dark, on logs which were badly attacked by the mycelium.

That the cultures here described failed to develop pilei in the light, must be attributed to conditions of culture, such as the very restricted air supply which is present in the tubes, and the comparatively small amount of food material present. Lakon (8) and Miss Bayliss (1, p. 8) have shown that there is undoubtedly an inhibitory effect on development connected with such a restricted air supply.

(*c*). *Effect of light and darkness on the pure cultures.* As the presence or absence of light, and the intensity of light has a direct effect on the growth and development of fungi in many cases, experiments were made to determine whether this mycelium showed such a response.

Three sets of conditions were used for this purpose: (i) bright light, in a large window with a north aspect; (ii) subdued light, in the same room at a distance of some feet from the window; (iii) darkness—almost continuous in a dark room, but unfortunately some dull light entered at times through the door being left open.

In one set of experiments cultures were set up on Lime wood and Sycamore wood on May 3. On August 6 the series in light showed a very feeble growth in every case, while, that in darkness showed a much stronger development.

Another series was set up on Elm wood, and cultures were kept under conditions i, ii and iii. The growth of the mycelium was strongest (externally at any rate) in the dark. The cultures in dull light showed a condition intermediate between these and the thin growths again obtained in bright light—often in the last case no more than a thin brown layer barely covering the surface.

Abnormal fructifications, as described above, were produced in nearly every case, on blocks kept in dull light. In no case were fructifications of any kind produced in bright light,[1] and in darkness only two structures appeared which may have been incipient fructifications.

Marshall Ward (14) in his work on *Stereum hirsutum* found that " light is not necessary to the development of the fungus or the hymenia " and apparently there were no noticeable differences between cultures kept under conditions of darkness or diffused light.

It is interesting to find in the present case that although light is not necessary for the growth of the mycelium, yet it has a strong influence on the actual development of the abnormal fructifications.

The more abundant growth of the mycelium in darkness seems to be due in part at any rate, to the retarding action of light on growth, a phenomenon of general occurrence (9, p. 98), so that the mycelium is feeblest when grown in bright light.

It seems that light is necessary for the formation of the fructifications, perhaps supplying a stimulus for their development. Buller, using naturally infected logs half destroyed by the mycelium of *P. squamosus* showed that up to a certain point development took place independent of light conditions (7, p. 57). The fructifications produced in the dark were always sterile, however, and highly abnormal in form, and Buller states that "the formation of the pileus is brought about entirely by a morphogenic stimulus of light."

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[1] See, however, the note at the end of this paper (p. 281).

In the cultures kept in darkness no fructifications were developed, with the possible exception of the two structures mentioned above. Hence it was the absence of light which probably caused the difference in the development of fructifications in the dull-light and dark series of cultures.

With regard to the cultures grown in bright light, possibly the mycelial growth was not active enough to produce fructifications in the given time. A direct retarding action of bright light is not likely in view of the occurrence of fructifications in conditions of bright light in nature.

(*d*). *Culture on other media.* The culture of the mycelium from the wood was tried in media consisting of a strong wood extract made into a stiff jelly with Gelatine or Agar. Cultures in Petri dishes and also on large surfaces of the medium in flasks were tried.

In the case of the Gelatine media, comparatively rapid liquefaction took place (6, p. 117), and the mycelia grew only slowly.

In Agar, the mycelia also grew very slowly, forming very thin cultures, and soon showing some slight oidial formation.

No further results were obtained from either of these methods of culture.

(*e*). *The formation of Oidia.* As already mentioned, the mycelia growing on wood, in nearly all cases produce bodies which seem from their method of formation to be "oidia." Cf. Brefeld (2, p. 203), Buller (6).

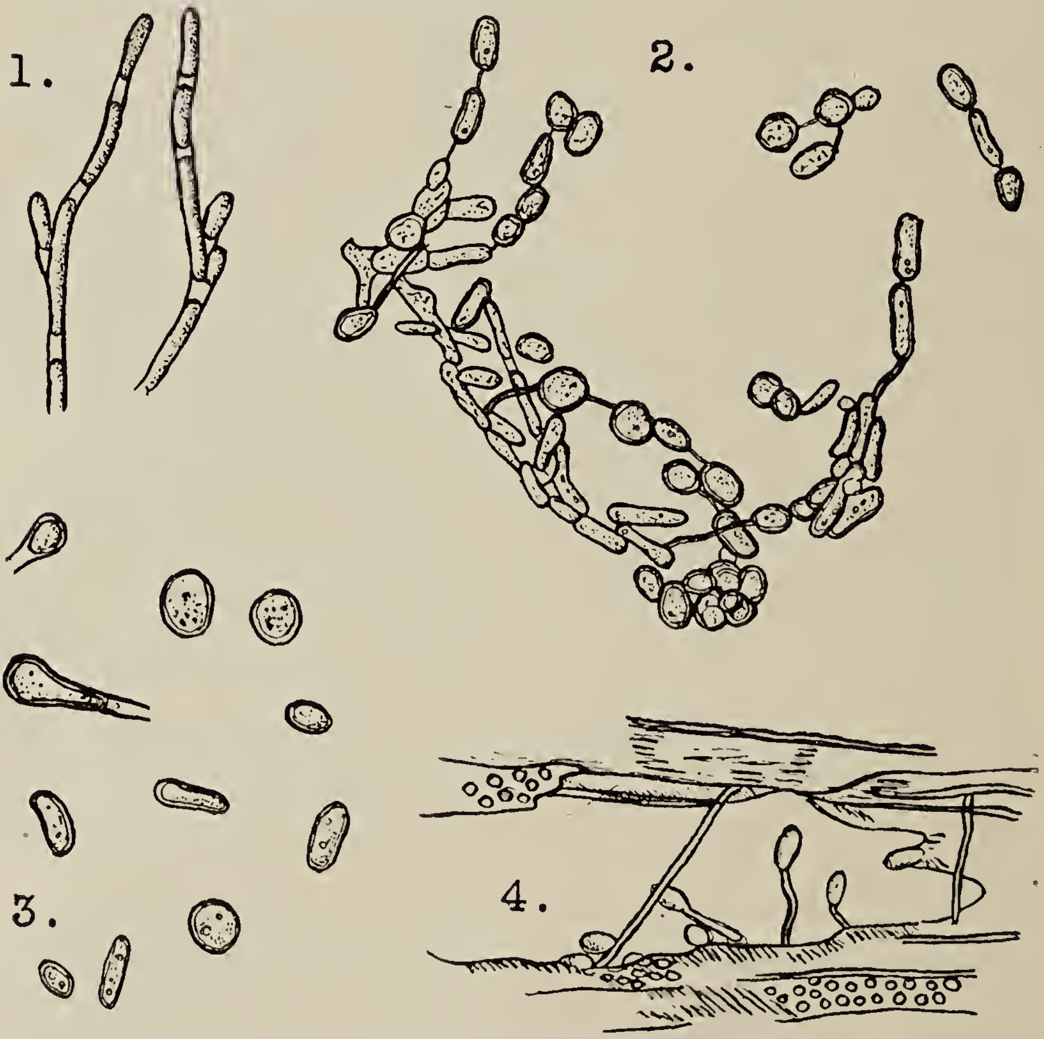
Their method of formation was made out by teasing the mycelium from regions close to those which were turning brown, and also in hanging drop cultures. Text-figs. 1—3 illustrate the mode of formation of the oidia.

The germination of the oidia, transferred from wood blocks to hanging drops of the following, failed in every case :—pure water, cane sugar, grape extract, Elm wood extract, water with sections of Elm wood.

In somewhat similar cultures of *Polystictus versicolor* Miss Bayliss (1, p. 3) found that oidia, of much the same type as these, were produced very sparingly and only in rare cases.

II. GERMINATION OF THE SPORES.

(*a*). *In hanging drops.* The results of attempts to germinate the spores in various media were closely similar to those obtained by Buller (5). The spores germinated readily in beerwort, fairly well in a solution containing peptone, grape sugar and potassium nitrate, and sparingly in a slightly alkaline extract of Elm wood No germination occurred either in distilled water, rain water, or in water containing sections of Elm wood. Germination was also tried in Ward tubes—where there is a more abundant supply of air—but with no marked difference in the result.



Text-figures 1 to 4. Text-fig. 1: formation of oidia in hanging drop in peptone solution, shewing early stage (X *c*. 500). Text-fig. 2: group of oidia from wood block, three months old, showing the remains of the hyphæ uniting the oidia into chains—in some cases the walls have thickened (X *c*. 500). Text-fig. 3: group of free oidia from wood culture, showing variation in shape and size (X *c*. 500). Text-fig. 4: spores germinating and penetrating elements of living tree: inoculated on new wound, November 20, 1912, cut November 27, 1912.

Spores which had been kept in a corked tube from November 11 to February 5—a period of 79 days—germinated quite well in beerwort, although there was a little delay in the first appearance of germ tubes. The spores are thus able to retain their power of germination for a considerable time under laboratory conditions.

(*b*). *Germination on wood.* On blocks of Sycamore and Horse Chestnut wood, Buller (6, p. 116) found that few spores germinated and penetration failed.

Since cultures had been raised from spores on wood, it was obvious that germination and penetration had taken place and in order to observe this the following method was employed. Slips of wood, about 12 mm. square were placed in small tubes on damp cotton wool and sterilised. Fresh spores were collected and a little heap was placed at the centre of each slip, and these tubes were left in a damp atmosphere.

They were set up on November 27, 1912. On December 3, a fair proportion of the spores was germinating, and little groups of tangled hyphæ were present, formed by the germination of a number of spores close together, more especially among those spores which had been in direct contact with the wood. On December 7 the spores were germinating fairly freely, but apparently with some irregularity, and tangled hyphæ of considerable length occurred. It did not appear, however, that any penetration of the wood had taken place. These cultures were re-examined on January 13, 1913, and were still pure. On examining a block under the low power of the microscope, the hyphæ could be seen as fine lines stretching from the heap of spores in abundance, and then apparently penetrating the surface of the wood. Many of the spores which were not in contact with the wood had failed to germinate.

On cutting sections of the blocks thus infected, near the region of the heap of spores, the hyphæ were seen to have penetrated the vessels and other elements of the wood. As soon as the hyphæ entered the wood, they followed more especially a longitudinal direction and were often present in large numbers in the vessels at some distance from the point of inoculation.

This appears to explain the tardy appearance of the mycelium on the wood blocks in tube culture. The spores germinate quite slowly, and instead of forming a layer over the surface of the wood, they at once make their way into the tissues. Only after some time does the mycelium on the surface grow enough to be obvious.

III. THE DESTRUCTION OF WOOD.

Buller has described the destruction of the wood of *Acer* by the fungus in nature. The hyphæ penetrate all the wood cells and delignify them. The fibres between the spring elements succumb earliest, the wall gradually disappearing from within towards the middle lamella, so that there is no separation of the elements.

In the present work an investigation was made of the earlier stages of the destruction of Elm wood induced by the fungus in pure culture.

The hyphæ were present in very large numbers in practically all the elements, to a depth of 5 to 6 mm., in the older culture blocks. The removal of the somewhat leathery mycelial felt from the block usually accomplished the removal of some of the disintegrated wood on the outside. Sections were cut in various directions and at different depths, the staining being usually effected by the use of Gossypimine (Cotton Red) and Picric Aniline Blue, or of Methyl Green and Congo Red (cf. 5, p. 176). With the first combination, the hyphæ stain a bright blue and the lignified portions of the section red.

Generally speaking the hyphæ were very few at depths greater than 6 mm., and were then usually most obvious in the vessels, as very fine straight threads. A few hyphæ penetrated the elements to the middle of many of the wood blocks examined. The medullary rays were almost constantly avoided by the hyphæ.

Potter (10) has shown that steam sterilisation may have the effect of delignifying the inner walls of some of the elements and that there is a considerable amount of cellulose lining the walls of the elements in fresh wood. He suggested that a portion of the delignification obtained by Marshall Ward (13) in his cultures of *Stereum hirsutum* may have been due to this effect. He, however, tried the effect of steaming only on thin sections and not on large blocks of wood. Spaulding (12) tried the effect of steaming on sections of some American woods, but found on the whole that little delignification took place, and he assumed that the delignification produced in culture blocks would be negligible.

For comparison with the culture blocks in the present case, blocks of Elm wood, similar to those used for the cultures, were set up steam-sterilised as before, and kept for some months in the damp atmosphere of the tubes. These blocks were used for comparison with the fresh wood, and with the wood attacked by mycelium.

To study the delignification, sections were treated with chlor-zinc-iodine, phloroglucin and aniline chloride, the first of these giving the best results.

The fresh wood of *Ulmus* shows some cellulose lining the inside of the walls of the fibres (10, p. 127). I find it more particularly in the fibres associated with the vessels.

There was apparently a little more cellulose present in the steam-sterilised wood than in the fresh wood, chiefly in the fibres of the spring wood of each year but the distribution was rather irregular. This may have been due directly to the steaming, or in part to the prolonged action of water on the wood.

The difference in wood, even slightly attacked by the fungus was obvious, and there was no doubt whatever, that a large amount of the delignification was actually caused by *Polyporus squamosus.*

The effect of the growth of the fungus for 9 to 12 months on a block of Elm wood is as follows:—

Just at the outside, for a depth of about 1·5 mm. the disintegration is advanced, the wood being soft and falling to pieces when cut with a razor. Sections of this outer region show a destruction similar to that observed in naturally attacked Elm wood. The vessels of the spring wood and a large number of fibres in their vicinity have completely broken down, but the autumn wood is only slightly attacked. The medullary rays are quite intact and serve to hold the bands of undestroyed wood together.

On cutting transverse sections which include the peripheral regions, from the middle of a block, the progress of the action is evident. Such a section, treated with chlor-zinc-iodine, shows on the outside the lignified skeletons of the fibres, practically no cellulose being present. It is quite clear that the cellulose has been absorbed by the mycelium. Inside this zone the amount of cellulose present is very striking. Practically all the fibres of perhaps one half the year's wood in each ring have their walls converted into cellulose, with the exception of a thin middle zone of the wall, the cavities being nearly occluded by this cellulose lining. Practically no cellulose was to be detected in the vessels, but these were the most rapidly destroyed and usually contained most of the hyphæ, so that it is possible that the cellulose is used here as rapidly as it is formed.

Considerable delignification was detected also in the centre of the blocks. Better conditions of aëration resulted in a more rapid penetration of the hyphæ.

The process of disintegration taking place here is on the whole similar to that described by Marshall Ward for *Stereum hirsutum*, the delignification taking place towards the middle lamella.

In the case of Coniferous wood, on which a sparse mycelial growth was obtained, very little destruction had taken place. The medullary rays here were specially liable to attack, and in fact contained most of the hyphæ which had entered. Hyphæ had also penetrated a few of the outer layers of tracheids, usually by means of the bordered pits. A little delignification had occurred in the elements thus attacked, but the amount of cellulose produced was not great and was quite confined to these tracheids.

IV. INFECTION OF THE LIVING TREES.

(*a*). *Mycelial Inoculations.* Apparently no successful infections of living trees have yet been reported.

To try to trace the method of infection and penetration inoculations were made on young Elm trees planted at the Botanic Garden, Cambridge. I should like here to record my thanks to Mr. Lynch, the Curator of the Garden, for his help in this connection.

In the first place inoculations were made on May 6, 1912, with pieces of mycelium grown in pure culture on Elm wood. The mycelium was placed in scalpel wounds made both on healthy and dead branches, the wounds being subsequently covered closely with tin-foil and bound with wool (cf. 4, p. 136). On July 5, two twigs were removed and examined for hyphæ, one twig having been dead at the time of inoculation, the other healthy. Hyphæ were distinctly but sparingly present in the dead twig, but no sign of hyphæ was found in the twig that had been living. The mycelium present in the dead twig had the characters of that of *P. squamosus* as appearing in the culture experiments, but there is the danger with a dead twig that hyphæ of another fungus may have already been present.

Another twig living at the time of inoculation was examined on October 12, and again no mycelium was found.

Mycelial inoculations were made on an old wound-surface and on one freshly made on the same living branch on October 18, 1912. The whole branch was removed on January 21, 1913, and the two inoculations examined. From the inoculation of the old wound-surface, hyphæ had penetrated the vessels and other elements of the wood fairly freely and had effected a radial penetration more than half way to the centre of the branch (about 9 to 12 mm. diam.) in the interval October 19 to January 21. The lateral penetration below the old wound was slow, and the hyphæ spread more quickly in a longitudinal direction, although during the interval October 19 to January 21 the hyphæ had spread only a distance of about 12 mm. above and below the limits of the inoculated surface. The hyphæ penetrate the vessels more freely than the other elements, We cannot be certain that these hyphæ belong to *P. squamosus* because the inoculated surface was an old one. Similar wounds, however, were examined and the amount of discoloured tissue below the wound-surfaces was much smaller than in the case of the one inoculated; hence it is a reasonable supposition that the greater discolouration associated with the inoculated wound was caused by *P. squamosus.*

Hyphæ had penetrated only to a slight extent the new wounds which had been inoculated, in fact they were only seen in the vessels quite close to the surface. Since both the wounds had been treated in exactly the same way, and had been subject to exactly the same conditions throughout, it appears conclusive that the nature of the wound has some effect on the rate of penetration. In the case of the old wound, possibly the layer of dead cells present on the outside forms a suitable substratum for the first growth of the mycelium. Or it may be that the living cells of the new wound have some direct toxic action on the growing hyphæ.

(*b*). *Spore inoculations.* Spore inoculations were made in the autumn of 1912 on the trees already mentioned. The spores were collected in large numbers, and placed on old and new scalpel wounds in large numbers in some cases, or mixed with sterile water, the inoculations being protected in the usual way.

A number of inoculations were made in this way on November 16 and also November 20, 1912. Those of November 20 were made with large quantities of spores. A twig was removed on November 22 (the wound was fresh at time of inoculation) and spores were washed off and examined. A very few out of the large number showed early stages of germination.

On November 27 the same method of examination was repeated for wounds of both types. None of the spores washed off showed any signs of germination, but on scraping off the surface, spores with long germ tubes were present fairly frequently (Text-fig. 4). It seems probable then that after nine days, these germ tubes were beginning to penetrate the wood. The hyphæ entered the vessels near the surface. The penetration of the mycelium from spore-infections was very slow. A freshly wounded twig infected with spores on November 16, 1912, shows hyphæ in only the three or four external layers of vessels by April 17, 1913.

SUMMARY.

1. *Polyporus squamosus* has been raised for the first time in pure culture on Elm wood blocks from the spores. The fungus has been grown also on other kinds of wood.

2. The mycelium grows slowly taking about two months to appear after spore-infection. "Oidia" are generally produced in large numbers by the mycelium, after a few months' growth.

3. Sterile fructifications of a peculiar form developed in a large number of cultures kept in dull light.

4. Mycelial growth was generally stronger in darkness than in dull light, and was much feebler in bright light. No fructifications were produced in cultures kept in darkness nor in bright light.

5. The germination of the spores and penetration of wood was followed on wood slips in pure culture.

6. The destruction of the wood by the fungus in pure culture was investigated. Considerable delignification occurred from the lumen outwards and the middle lamella remained intact.

7. Inoculations of Elm trees, both with mycelium from pure culture and also with spores, have been made.

In conclusion, I wish to record my very best thanks to Mr. F. T. Brooks for his continued interest and help in the work, and also to Mr. C. G. P. Laidlaw for help with the photographs.

BOTANY SCHOOL,
CAMBRIDGE.
June, 1913.

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DESCRIPTION OF PLATE VI,

ILLUSTRATING MR. PRICE'S PAPER "ON *POLYPORUS SQUAMOSUS* HUDS."

Fig. 1. Four cultures showing fructifications which are chiefly of the branched type.

Fig. 2. A larger view of a similar type, showing the characters of the mycelium and the exudation of liquid drops towards the base.

Fig. 3. Mycelium on the wood of *Pinus*. Note the very sparse growth here obtained.

NOTE ADDED SEPTEMBER 25TH, 1913.

Since the above was in the press, one of the cultures in bright light has produced an interesting fructification. This culture was further nourished by pouring into the tube some of the peptone containing solution already mentioned. The fructification is long and stalk-like, but is slightly spathulate and flattened at one end, while on one surface is present a system of irregular pores, much resembling those which occur at the base of the normal *Polyporus* fructification. There is thus reason to hope that this fructification will be found to have produced a hymenium, and possibly basidiospores, but it has not yet been examined for this.

Thus, as was surmised above, bright light cannot have any direct inhibitory effect on the development of the fructifications.

THE DETERMINING FACTORS IN PETIOLAR STRUCTURE.

BY E. J. SALISBURY, B.SC.,

East London College, University of London.

THE organisation of the petiole is intimately related to that of the leaf which it bears and we should expect, on *à priori* grounds, that variations in the structure of the one would be reflected in those of the other. One of the most important questions that arise in this connection is how far differences in the potentialities for transpiration between leaves of the same species, or those of different species, affect their respective vascular organisations.

The amount of the conducting tissue has perhaps been too much overlooked as a factor in transpiration, for given a constant suction force, the rate of flow will be dependent upon the size and number of the supplying tracheæ. In the present paper some of the preliminary results obtained in an investigation of the above considerations are given. The work was begun as an outcome of the author's results[1] in connection with the extrafloral nectaries of *Polygonum*, but owing to the difficulties experienced in finding a fully reliable method of estimation and the time involved in obtaining a single result the data brought forward are fewer than the author would have wished, but it is hoped at a future date to multiply the evidence here adduced. Comparatively little work having a direct bearing upon this subject has as yet been done. Kohl,[2] working on the stems of *Hedera helix*, *Mentha aquatica*, *Thalictrum galioides*, and other plants shewed that the bundles, as a whole, of plants grown in a damp atmosphere were smaller in size than those of other plants of the same species grown in a dry atmosphere. Jost[3] experimenting upon the bean seedling found that removal of a cotyledon caused the corresponding bundles to remain rudimentary, whilst the severing of an individual strand caused its abortion below, though continuing its development above. Schacht[4] had also made an observation of interest in this connection namely that in the saprophytic *Epipogon gmelini* the leaves are without stomates, and associated with this feature no vascular system is developed. At the time of writing, a paper has appeared by Hill and de Fraine[5] in which a relation is shewn to exist between the area of cotyledons and their vascular supply as a whole.

From these scattered observations it is at once apparent that there is a general relation existing between transpiration and the development of vascular tissue. In 1886 Darwin and Phillips[6] shewed the importance of the cross sectional area of the conducting lumina of the vessels by their experiments upon compressed and bent stems which exhibited a diminution in the transpiration current.

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[1] Ann. Bot., Vol. 23, 1909, pp. 229-242.

[2] "Transpiration der Pflanzen," 1886, p. 116, Pls. II-IV.

[3] "Ueber Beziehungen zwischen der Blattentwickelung und der Gefass bildungen in der Pflanzen." Bot. Zeit., Bd. 51, 1893, pp. 85-134.

[4] "Beiträge zur Anatomie und Phys. der Gewächse," 1854, p. 115.

[5] "A consideration of the facts relating to the structure of seedlings." Ann. Bot., Vol. 27, pp. 257-272, 1913.

[6] "On the transpiration stream in cut branches," Proc. Comb. Phil. Soc. Vol. 5, p. 364.

In order to ascertain how close was this relation the total cross sectional area of the lumina of all the tracheæ in various petioles was estimated and the relation which the figures so obtained bore to the periphery (in still air) or the area (in moving air) of the respective leaves was calculated.

For this purpose transverse sections of the petioles were cut at corresponding levels and stained for xylem only, being afterwards cleared and mounted in balsam. They were then projected by means of a microscope and suitable optical system on to a screen at right angles to the axis of light so that a magnification of some 800 diameters was obtained.

The area of the lumen of each vessel was then traced and afterwards transferred so that those of each petiole together formed a continuous figure resembling a necklace. In this way the area was rendered sufficiently large to be accurately determined by means of a planimeter.

Before discussing the actual figures it will be well to deal with a few theoretical considerations.

Brown and Escomb have demonstrated that in still air the evaporation from a circular area is proportional to its diameter whilst if the water vapour be removed by wind the evaporation varies directly as the area. Either of these ratios, however, involves the assumption of an ideal condition for its absolute fulfilment, in the one case perfect stillness in the other equally perfect removal.

In nature there is probably always more or less of a vapour cap covering the stomatal surface especially as the latter is most frequently confined to the under side of the leaf. In exposed situations the vapour cap is retained by means of transpiration checks or the rapidity of diffussion is lessened by the thickness of the leaf which as Renner[1] has shewn shifts the plane of saturation some way from the external surface. The maximum rate of transpiration for any leaf in moderately still air will then be broadly proportional to the periphery and the more rapid the movement of the air currents the closer will the approximation become proportional to the area.

In order to eliminate as far as possible errors due to development under differential treatment the bulk of the observations have been made upon greenhouse plants, and by choosing those with opposite leaves and comparing the members of each pair, differences due to age are largely eliminated.

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[1] "Beiträge zur Physik der Transpiration." Flora, Bd. 100, pp. 451-548, 1910.

It will be seen from the subjoined table that the ratio given by dividing the length of the periphery of the leaf by the total cross sectional area of the vascular lumina is so close in the majority of cases between individual members from the same node, that we can only conclude a definite relation exists between the transpiring surface and the xylem development. The ratio is seen to vary within the species as much as 22%, but as between distinct species the differences are very much greater. The maximum divergence amounting to 3,000% is shewn by *Clematis* on the one hand and *Bignonia* on the other.

GREENHOUSE PLANTS. TRANSPIRATION OF PERIPHERY.

Clematis sp. (mesophyte).

Leaf.	Measurement of periphery $=p$.	Xylem area $=x$.	No. of Vessels.	Ratio $\frac{p}{x}$
A	37·8 cms.	6·35 sq. mm.	216	5·7
B	33·6 ,,	5·78 ,, ,,	193	5·8
C	34·2 ,,	6·30 ,, ,,	194	5·4
D	34·2 ,,	6·04 ,, ,,	160	5·6
E	30·8 ,,	6·33 ,, ,,	171	4·8
F	30·0 ,,	6·88 ,, ,,	160	4·3

Bignonia sp. (small leaved with hairy surface).

Leaf.	Measurement of periphery $=p$.	Xylem area $=x$.	No. of Vessels.	Ratio $\frac{p}{x}$
A	24·4 cms.	0·116 sq. mm.	73	210
B	20·5 ,,	0·095 ,, ,,	75	215
C	22·1 ,,	0·099 ,, ,,	77	223
D	21·0 ,,	0·097 ,, ,,	63	216
E	22·4 ,,	0·108 ,, ,,	91	207
F	21·4 ,,	0·104 ,, ,,	78	205

Clerodendron sp.

Leaf.	Measurement of periphery $=p$.	Xylem area $=x$.	No. of Vessels.	Ratio $\frac{p}{x}$
A	21·1 cms.	1·93 sq. mm.	50	10·9
B	18·7 ,,	1·76 ,, ,,	63	10·6
C	18·4 ,,	2·00 ,, ,,	60	10·8
D	15·5 ,,	1·71 ,, ,,	61	11·0
E	20·5 ,,	2·58 ,, ,,	70	12·5
F	18·0 ,,	2·47 ,, ,,	40	13·7

Now a small ratio signifies that the value of x is large, or in other words, there is more xylem for each unit of leaf effectiveness, a condition we should expect to find where the rate of evaporation is fast. If the ratio be large as with *Bignonia* then less xylem corresponds to the same unit.

Now of the species in question the *Clematis* was a large smooth leaved mesophytic plant, whilst the *Bignonia* had leaves of small area and possessed an effective transpiration check in the form of copious hairs. We thus see that there is also indicated a correspondence in xylem development according as the species transpires, rapidly or slowly.

In fairness it should be said that attempts have been made to estimate the transpiration of individual leaves so that direct comparison with the xylem development could be made, but up to the present the results obtained have been worthless as the ratio between the transpirations of the different leaves, although the experiments were prolonged over several days, did not remain constant. If however such a definite relation does not exist, the results here obtained are inexplicably constant.

With regard to the failure to obtain direct results it must be borne in mind that any method of ascertaining the transpiration of a leaf after removal from the plant is open to the same objections as those raised by Dixon[1] for separated branches. Further, such methods give us the transpiration for the conditions under which the experiment is conducted, which are the same for all the leaves. But it is doubtful whether, when the leaves are upon the plant, the average maximal conditions for transpiration are the same for any two leaves. So that it is conceivable that whilst in nature two leaves of similar size may transpire at very different rates, under experimental conditions the relation between them becomes either lessened or even in extreme cases inverted.

The experiments of Dixon (Proc. Roy. Soc., Lond., B, 1907), Ewart (Phil. Trans. Roy. Soc., Lond., B, 1905) and others upon the resistance offered to the passage of water through wood, ranging from a head just over one, to as much as thirty-three times the length of the stem, have shewn how great is the influence of the rate of flow upon the resistance. Where the flow is normally rapid this increased resistance is neutralised by an increase in the size of the vessels. The large size of the lumina of the vessels constituting the spring as compared with the autumn wood is an accompaniment of the periodic change in the rapidity of the transpiration current, and a comparison of the vessels of mesophytic and xerophytic plants shews the same relation. Similarly in the development of the leaf itself the xylem of the immature condition is composed of tracheæ which have a larger average lumen than those of the adult.

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[1] "Transpiration and the Ascent of Sap." Progressus rei Botanicæ, Band 3, Heft 1, 1909, p. 59.

A temporary excess over the average maximal transpiration provided for will of course be met by a corresponding closure of the stomatal mechanism, but if this condition continues as a permanent change the decreased rate of flow in the transpiration current (reacting perhaps upon the food-supply, Jost, loc. cit.) probably acts as a stimulus to the production, by the developing leaves, of an augmented conducting system.

Sinnott[1] observes that "it is a noteworthy fact that in very many ferns the leaf becomes slender at its attachment and that in almost all of them the vascular supply, besides being much less complicated at this point than higher up the petiole, is also composed of a much smaller number of cells." He concludes therefore that it is "extremely doubtful if the size of the transpiration current has had much influence on the development of the vascular supply."

The writer has confirmed the above generalisation for several species of ferns and it was found that in a *Polypodium* sp. the total cross-sectional area of the xylem in the middle region and in fact throughout the greater part of the petiole was about 0·026 sq. mm. At the base, however, the area was only 0·011 sq. mm. or a reduction of nearly 60%. In *Clematis aristata* a similar reduction was found at the extreme base of the petiole, the area throughout the greater part was ·0385 sq. mm. and at the base 0·364 sq. mm. Also this divergence is to some extent increased by the larger size of the vessels in the upper part (·000447 sq. mm.) as compared with the lower (·000327 sq. mm.)

In every case examined, however, the marked contraction is confined to a *short* distance at the *base of the petiole*. Mr. Ormsby, who has worked on the effect of contraction in water mains, has, however, shewn that where the length of contraction is small as compared with the total distance traversed the effect is negligible (see Middleton, "Water Supply," pp. 152-153). Hales ("Vegetable Staticks," Ed. 2, 1731, p. 138, Exp. XLV) records the observation that the leaves of a branch from which the outer wood had been removed for a short distance withered no sooner than those on other branches. Also Darwin and Phillips (loc. cit., p. 339) found that a single cut beyond the centre of a stem produced no very great diminution in the rate of absorbtion. In experiment 5 (p. 341) a diminution of the area of the conducting surface by more than one half only produced a diminution in the absorbtion of about 6%.

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[1] The Evolution of the Filicinean Leaf-Trace." Ann. Bot., Vol. 25, 1911, p. 187.

It is clear then that the principles that obtain in water mains hold good for the translocation of water in plants and that local variations where they only extend over a short distance do not appreciably affect the final result.

As Dixon has pointed out the water column in a plant is continuous and therefore the presence of numerous walls, though introducing a resistance factor does not invalidate comparison with a single water channel. Approaching the problem from another standpoint leaves from two plants of *Stachys sylvatica*, one of which was a shade-form and the other a sun-form, were compared in order to see whether the different capabilities of transpiration were reflected in the xylem development, for as Wiesner[1] shewed, under the same conditions shade-leaves transpire more than sun-leaves. The leaves were taken from different nodes so that very close relations between the ratios are not to be expected. As the material was obtained from the natural habitat the areas of the leaves, not the peripheries, have been used in calculating the ratios.

Sun Leaves.	Shade Leaves.	Area of Leaf.	Area of Xylem.	Ratio $\frac{l}{x}$
	Leaf *a*	54·41 sq. cms.	·03408 sq. mm.	15·9
Leaf *b*		48·06 ,, ,,	·03271 ,, ,,	14·6
	Leaf *c*	47·72 ,, ,,	·03207 ,, ,,	14·91
Leaf *d*		39·53 ,, ,,	·0293 ,, ,,	13·4
	Leaf *e*	36·62 ,, ,,	·0275 ,, ,,	13·31
Leaf *f*		28·97 ,, ,,	·0228 ,, ,,	12·7
Leaf *g*		25·63 ,, ,,	·0226 ,, ,,	11·3
Leaf *h*		22·85 ,, ,,	·0222 ,, ,,	10·2
	Leaf *i* (very young)	11·32 ,, ,,	·0183 ,, ,,	6·1

Comparing leaves of similar dimensions it will be seen that the ratios given by leaves *b* and *c*, and *d* and *e* are very close which fact points to the different potentialities for transpiration between sun- and shade-leaves being such that under their natural conditions of growth the differences in humidity of the habitats are almost exactly equalised. Comparing the sun-leaves *f*, *g*, and *h*, it is seen that with the increase in size of the leaf there is a gradually increased ratio. This may well be due to the fact referred to above that even in moving air the leaf is to some extent covered by a vapour cap so that the evaporation is proportional to some figure whose value lies between that of the periphery and the area.

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[1] "Photometrische Untersuchungen auf Pflanzenphysiologischen Gebiete." Sitz.-ber. d. k.k. Akad., Wien, 1893.

In the great majority of Dicotyledonous plants the increase of xylem within the petiole accompanying increase in size of the leaf is brought about by secondary thickening. But in such plants as the Polygonaceæ the activity of the cambium is either very slight or absent altogether so that with the increase of leaf-area we find an increase in the number of bundles which the petiole contains. In the following table the number of vascular strands in leaves of *Rheum* and *Rumex* of different sizes is given. As will be seen there is a general correspondence which if the size of the individual bundles had been considered would have been found to be very much closer.

	Size of Leaf.	No. of Bundles.
Rheum. Mature leaves *a*	6247 sq. cms.	300
b	4513 ,, ,,	272
c	3523 ,, ,,	246
d	2155 ,, ,,	191
e	690 ,, ,,	90
f	510 ,, ,,	83
(immature) *g*	284 ,, ,,	93
Rumex *a*	320 ,, ,,	30
b	175 ,, ,,	17
c	100 ,, ,,	15
d	100 ,, ,,	16

Darwin and Phillips shewed that the bending of a stem had a marked effect upon the transpiration current, a fact which we find expressed in the large size of the conducting channels of climbing plants. It is therefore of importance to the plant that the petioles should withstand strains, which will be more or less proportional to the areas of the leaves they bear.

For purposes of comparison the strength of the petiole has been assumed to be proportional to its breaking strain. In order to calculate the latter the petiole was supported by a slotted plate, and a band the width of the slot passed over it and attached to a vessel of known weight. Water was gradually added in such a way that immediately the petiole broke the stream passed outside the vessel owing to its descent. The water was then measured and its weight added to that of the receptacle. The results obtained shew that a considerable degree of relationship exists between area and breaking strain and therefore presumably resistance to bending.

Species.	Area of Leaf.	Breaking Strain.
Polygonum cuspidatum Plant A	180 cms.	133 ozs.
,,	168 ,,	116 ,,
,,	94 ,,	98 ,,
,,	58 ,,	67 ,,
Plant B	164 ,,	125 ,,
,,	144 ,,	119 ,,
,,	70 ,,	72 ,,
,,	66 ,,	58 ,,
Aucuba A	103 ,,	121 ,,
,,	70 ,,	103 ,,
,,	49 ,,	80 ,,
Aucuba B	79 ,,	84 ,,
,,	54 ,,	68 ,,
Helianthus	181 ,,	176 ,,
,,	104 ,,	83 ,,
,,	52 ,,	53 ,,

Many observers have called attention to the utility of the open arc arrangement of the vascular bundles in maintaining the rigidity of the petiole in unilateral leaves, and this is still further emphasised by the flattening out which the arc shews in the adpressed radicle leaves of many species. Also in leaves such as *Hydrocotyle*, *Tropæolum*, *Oxalis*, *Pterospermum acerifolium*, *Hernandia ovigera*, etc., where there is either a complete ring of xylem or the bundles are symmetrically arranged, we see a definite relation to the almost equally distributed strain. A similar phenomenon is exhibited by many pseudo-peltate leaves, e.g,, *Geranium* spp., *Malva rotundifolia*, etc., where although the leaf is morphologically unilateral, mechanically it is radially symmetrical.

From these preliminary observations we can only conclude that the functions of the leaf have a profound influence both upon the amount and arrangement of the xylem. So that whether we be concerned with the petiolar structure of the mature organism or with that of the cotyledons, it is to function, rather than to phylogeny, that we must look for its elucidation. In so far as the vascular system of the stem is itself built up of leaf-traces the same generalisation will apply with equal force. Even in those cases where a special cauline vascular organisation is present the same regulative factors may well have determined the limits of development.

RECENT PAPERS ON *ŒNOTHERA* MUTATIONS.

By R. Ruggles Gates, M.A., Ph.D.

SINCE the publication of De Vries's mutation theory the investigations with *Œnothera* have become manifold, and have included almost every phase of the subject which bears in any way on genetic research. The Œnotheras have been and are still being closely examined from every point of view which may throw light upon their peculiar and complex behaviour. As a result of these extensive investigations of the phenomena of heredity and variation, as well as of the cytology, distribution, systematics and various other features, the mutating Œnotheras are perhaps better known than any other group of plants of corresponding size.

The accumulated data of the last decade have added much to the complexity of the facts, without, in many cases, an equivalent amount of explanatory simplification. Many of the hybridization results are now, however, becoming more clarified,—at least in the sense that they are seen to be consistent with each other,—while the cytological work has been most serviceable in furnishing an explanatory basis for the mutation phenomena themselves, removing some of these problems from the region of speculation to that of fact.

The papers on *Œnothera* have become so numerous in recent years that a complete bibliography of the subject is already a somewhat extensive undertaking, so I shall mention only certain of the more recent papers to indicate the later results and the present position of investigation in this subject. The contributions for the most part group themselves as dealing with (i.) the heredity and variation, (ii.) the cytology and (iii.) the systematics of the group. We may therefore conveniently consider them in that order in part, though the close relationship between the cytological and breeding results in this genus makes it quite impossible to deal with these two phases independently of each other. Indeed, the Œnotheras furnish the best example we have in plants, of the manner in which hybridization and microscopic study should go hand in hand in attempting an explanation of hereditary phenomena.

The breeding experiments with *Œnothera* have been greatly extended in scope since the publication of *Die Mutationstheorie* by De Vries, and I shall only mention a few of the papers on this subject. Extensive crossing experiments have been carried on, not only with *Œnothera Lamarckiana* and its mutants, but with various races of *O. biennis*, *O. grandiflora*, *O. muricata*, *O. Hookeri* and other species.

The earlier crosses made by De Vries among the mutating forms showed a variety of types of behaviour, the peculiarities of which have since been explained in part by the cytological results. When such mutants as *rubrinervis*, *nanella* and *lata* are crossed with *Lamarckiana* the F_1 contains both parent types in varying proportions, and in the first case both these types breed true. On the other hand, when *Lamarckiana* is crossed with its putative derivative *brevistylis* the latter behaves as a simple Mendelian recessive; and the new characters in the mutant *rubricalyx* behave as a simple Mendelian dominant in relation to its parent *rubrinervis*. Again, *gigas* × *Lamarckiana* according to De Vries yields an intermediate race which remains constant, though in some cases the behaviour is more variable, depending apparently on chromosome mechanisms. These three types of hereditary behaviour are doubtless indicative of different types of germinal change involved in the origin of certain mutants, a view which is fully corroborated by the cytological evidence.

As regards interspecific crosses in *Œnothera*, the most important paper which has yet appeared is that of De Vries (11) on double reciprocal hybrids between certain races of the Linnæan species *O. biennis* and *O. muricata*. In general, it was found that both reciprocal crosses yielded uniform but strongly patroclinous hybrid races which remained true in later generations. These reciprocal crosses, which were therefore unlike, were in 1908 reciprocally crossed with each other, i.e. (*biennis* × *muricata*) × (*muricata* × *biennis* and (*muricata* × *biennis*) × (*biennis* × *muricata*). In both cases the offspring were a uniform race corresponding with the "outside grand-parents." Thus (B × M) × (M × B) gave B or *biennis*, while (M × B) × (B × M) gave *muricata* which remained constant. The double reciprocal crosses therefore gave complete reversion to one of the grandparents, while the characters of the grandfather could not be transmitted through the mother and those of the grandmother could not be transmitted through the father. Similar results were obtained in crosses between races of *O. biennis* from Holland and Illinois, also with *biennis* and *cruciata*, *biennis* and *strigosa*, *biennis* and *Hookeri*, and *biennis* and *Lamarckiana*. In the *biennis-muricata* series of hybrids, what are called sesquireciprocal crosses were made, thus (*muricata* × *biennis*) × *muricata* [=(M) B × M] and (*biennis* × *muricata*) × *biennis* [=(B) M × B]. The former of these crosses is again identical with *muricata*, and the latter with *biennis*. Iterative hybrids were also produced in the following manner: (M) B × B and B × (B) M, etc. The iterative hybrids were like their hybrid parent. Thus (M) B × B=(M) B and B × (B) M=(B) M.

An ingenious explanation of these curious results has since been offered by Goldschmidt (23) whose interpretation is based on cytological study of these hybrids. Goldschmidt believes that a condition of merogony exists, the male nucleus developing in the cytoplasm of the egg, the nucleus of the latter degenerating. The cross *biennis* × *muricata* would therefore contain in its cells a *muricata* nucleus and *biennis* cytoplasm, while the cells of *muricata* × *biennis* would be derived from a *biennis* nucleus embedded in *muricata* cytoplasm. It is of course well known that the so-called "male cell" in Angiosperms is really a male nucleus which has lost its cytoplasm.

If the explanation of Goldschmidt proves to be correct, then these hybrids will furnish conclusive proof of the predominating influence of the nucleus in inheritance, for in each case the hybrid strongly resembles the parent from which its nucleus was derived.

Although the evidence for Goldschmidt's view is by no means complete and final, yet it establishes a certain presumption in its favour. Among the points figured are (i.) the degeneration of one of the nuclei (presumably the female) in the fertilized egg; (ii.) the apparent presence of only 7, the x number of chromosomes, in the cell-divisions of the embryo; (iii.) the smaller size of the embryo and its cells and nuclei in *biennis* × *muricata* than in *biennis*, which would be anticipated according to Boveri's law. Nevertheless, there are various difficulties, and the results of a fuller study of the subject will be awaited with interest. A number of other questions remain to be solved. If the hybrid embryo begins its divisions with only 7 chromosomes it is not probable that this number persists throughout the sporophyte, and Goldschmidt believes he has found evidence that the $2x$ number is restored in the later mitoses of older embryos. This introduces difficulties, however, for it is scarcely probable that all the cells would double their chromosome-number simultaneously, and if both types of cells continued we should anticipate as a result various distortions or changes in the shape of organs, for we should have different chromosome-numbers in different parts of the individual. The manner of chromosome pairing in meiosis would also be of interest, though we might anticipate the formation of seven pairs by analogy with the chromosome behaviour in the tetraploid mutant *gigas*. If more critical study sustains Goldschmidt's foreshadowing, we shall be able to add one more to the number of cases in *Œnothera* where cytological research has furnished the key to certain otherwise obscure or inexplicable hereditary phenomena.

It is worthy of mention that these reversions to one of the grandparents in double reciprocal crosses were predicted by Giglio-Tos (22) on generalized highly theoretical grounds concerning the structure and arrangement of protoplasmic elements, but it is highly improbable that this type of hereditary behaviour will be found to be common even in the genus *Œnothera* itself.

If Goldschmidt has correctly ascribed these results to merogony,[1] then a similar explanation may be applied (as that author has already done) to the various cases of "false hybrids," such as the well known results of Millardet with strawberries. In this case the hybrids were found to be all purely paternal in character and to breed true. The converse condition known in various Orchids, in which the hybrids are purely maternal in type, may conceivably result from the degeneration of the male nucleus after entering the egg or, as has often been suggested, from stimulation of the egg to parthenogenetic development by the presence of the pollen-tubes.

Another series of interspecific crosses has been made by Davis (7, 8, 9). He chose races of *O. biennis* from Massachusetts and of *O. grandiflora* from Alabama for the parents of his crosses, in the hope of producing *O. Lamarckiana*. But it must be said that from this point of view the results have not been successful. Hybrid forms were obtained, some of which showed a certain amount of crinkling of the leaves, but that is only one of many features of *O.*

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[1] Since the above was written, Renner ("Über die angebliche Merogonie der Œnotherabastarde," Ber. d. deutsch. bot. Ges,, Bd. 31, pp. 334-335, 1913) has re-investigated the subject in *O. muricata* × *O. biennis*, *O. biennis* × *O. Lamarckiana* and *O. Lamarckiana* × *O. biennis*. He finds the usual double fertilization in all cases, with $2x$ chromosomes in embryo and endosperm. Re-examination of Goldschmidt's preparations leads to the same result, so it must be concluded that there is no evidence for the theory of merogony in these hybrids as expressed by Goldschmidt.

Lamarckiana and one which is furthermore present in varying degrees in various *Œnothera* races. The flowers of the *Lamarckiana* of De Vries are distinctly larger than those of the *grandiflora* forms from Alabama. The F_1 hybrids of Davis were, however, (as would be anticipated) intermediate in flower-size between *grandiflora* and the small flowers of *biennis*, the intermediacy also extending to all the other characters, though forms with larger flowers have been obtained in later generations. The reciprocal crosses were made, *biennis* × *grandiflora* yielding eight plants, seven of which resembled *grandiflora* and were therefore patroclinous while one exhibited a certain amount of crinkling of the foliage. *O. grandiflora* × *biennis*, from the same parent individuals, produced twenty plants which were in two groups (twin hybrids), nine being *grandiflora*-like in foliage and habit while eleven resembled *biennis.*

Larger cultures of these F_1 and F_2 hybrids from fresh crosses were made in 1910 and 1911. The chief defect of these papers as descriptions of the hybrids is that the search for *Lamarckiana*-like plants among the offspring was allowed to overshadow the really more important general results of the crosses, since it was not to be expected in any case that *Lamarckiana* could have resulted from a single simple cross. In his last paper on these hybrids Davis virtually admits the correctness of this position.

In 1907 De Vries first described twin hybrids (*læta* and *velutina*) in the F_1 when *Lamarckiana* is used to pollinate *biennis*, *Hookeri* and other species. Notes on the anatomical features of these hybrids have been published by Andrews (1). The hybrid types both breed fairly true when self-pollinated. This hybrid behaviour has been confirmed by Gates (21) in the case of *biennis* × *Lamarckiana*, with full illustrations of the broad-leaved and narrow-leaved forms. Corresponding results were also obtained with *biennis* × *lævifolia.* It therefore appears that in *Lamarckiana* and its mutant derivatives, including *lævifolia*, the pollen grains are of two types, leading to a constant dimorphism in the F_1 of the hybrids when these forms are used as male parent. In the reciprocal crosses, however, De Vries obtained a single constant race, indicating an absence of this type of dimorphism in the egg-cells of *Lamarckiana*, though these results have not been fully corroborated by the later investigations.

This short review of the more recent hybridization results is necessarily very incomplete, but even a general summary of the data involved would be much too lengthy for the present purpose. The results show clearly, however, that several types of hereditary behaviour exist, and that these types depend upon the manner of origin and hence the relationship to each other of the various races and species concerned. Certain crosses give blended inheritance, others give alternation or segregation, others twin types unlike either parent, etc. A knowledge of the cytological conditions is necessary for an explanation of the hereditary behaviour of such mutants as *gigas* and *lata*, and also apparently of the results of certain double reciprocal crosses. In conjunction, these two classes of data furnish a consistent and rational view of very complex and sometimes apparently conflicting phenomena.

In connection with the twin hybrids produced by *Lamarckiana*, Honing (25) has made an interesting comparison of *Lamarckiana* and *rubrinervis*, treating them both anatomically and chemically. He points out that the differences between *Lamarckiana* and *rubrinervis*, are analogous to those between the twin types *læta* and *velutina* produced in such a cross as *biennis* × *Lamarckiana*; and he believes that *Lamarckiana* and *rubrinervis* are each under certain circumstances capable of giving rise to the other. This view is borne out by certain results of the reviewer. It is also of interest that several collections of wild seeds of *O. muricata* from widely sundered parts of Canada show a corresponding dimorphism (21), indicating that such a condition may be widespread in this section of the genus.

Three cytological papers have been published by Davis (4, 5, 6) which are in large part a confirmation of the earlier results of Gates (13a, etc.) It was found, however, that in *O. grandiflora* the pairing of the chromosomes in synapsis was closer than in either *biennis* or *Lamarckiana*, closed rings being formed by the chromosome pairs in diakinesis, while in the latter two species and their derivatives the homologous chromosomes are very loosely paired or not paired at all at that time. Hence it appears that the attraction which causes pairing is greater in *O. grandiflora* than in the other species. As I have pointed out, the loosely paired condition gives greater opportunity for irregularities, such as actually occur, in the distribution of chromosome pairs during meiosis. It is now certain that this process is concerned in the appearance of some of the mutations (*lata* and *semilata*).

In a detailed account of somatic mitoses in *Œnothera*, Gates (17) found the number of chromosomes in an individual to be constant, the rare exceptions in metaphase groups being explicable in entire accord with the belief in the genetic continuity of chromosomes from cell to cell. Certain peculiar cases were found in the cells of the nucellus in *O. lata*, in which the chromosomes were closely paired in metaphase as though about to undergo a reduction-division, though the chromosomes retained their somatic shape.

Several recent papers have dealt with the question of the origin *O. gigas*. There have been two chief views on this subject. Gates, in 1909, in showing the increased size of the cells and nuclei in *gigas* as compared with *Lamarckiana*, indicated the probability that the chromosome-doubling to give twenty-eight occurred in the fertilized egg or the young embryo, through a suspended mitosis. It was further pointed out that in various wild species the $4x$ number of chromosomes had probably originated in the same way. Strasburger (30) entirely concurred in these views and extended them to cover many new cases of $4x$ or tetraploid species. In a subsequent paper, Gates (20) has brought together a list of over thirty cases of tetraploidy, natural or experimental, in plants and animals. Tetraploidy is therefore a well recognized evolutionary condition, and many new cases will doubtless be found when the chromosome numbers of more plants are known. The gigantic character of the cells in *O. gigas* accounts for most, though probably not all, the peculiarities of this mutant.

The manner of origin of the tetraploid condition becomes, therefore, a matter of much interest. In addition to the view expressed by Gates and afterwards by Strasburger, Stomps (28) and Miss Lutz (27) have suggested another method, namely that tetraploidy in *O. gigas* originates from the chance union of two unreduced or diploid germ cells. In support of this view these investigators announced independently the discovery of triploid or $3x$ mutants having twenty-one chromosomes. Stomps found one such mutant from *Lamarckiana*, which he calls *semigigas*; and eleven Hero or $3x$ mutants from *Lamarckiana* and its mutants *rubrinervis* and *lata* pollinated by *cruciata*, *muricata*, *biennis* or *Millersi*. The frequency of triploid forms in these crosses (they were easily recognizable by their larger size and deep green colour) was about three per thousand. But it seems probable that these triploid mutants have all originated from the fertilization of a $2x$ (diploid) egg by a normal or haploid pollen grain, especially as in the reciprocal crosses triploid forms do not appear to have been found. These crosses do not therefore, as Stomps has supposed, furnish evidence of the occurrence of diploid pollen-grains. The same is true of the eight triploid mutants obtained by Miss Lutz. They may all have come from $2x$ eggs fertilized by pollen-grains having x chromosomes.

There is, furthermore, no observational evidence of the existence of diploid pollen-grains, though the megaspores which have been much less studied have furnished a case (Geerts) of a megaspore mother-cell of *Lamarckiana* having twenty-eight chromosomes. I pointed out (16) the probability that such a cell would develop an embryo after omitting both reduction and fertilization, and that *gigas* mutants may therefore originate in this manner. It has also been pointed out (20) that the occasional rare pollen-grains of *Lamarckiana* which, like *gigas*, have four lobes instead of three, may be diploid in chromosome-content. But there is at present no evidence that such pollen-grains are functional. The exact manner of origin of *gigas* hence remains uncertain, though it is possible that both methods of origin may occur. The discovery of triploid mutants, however, indicates the sporadic occurrence of diploid eggs in *Lamarckiana* and its derivatives, though there are of course other conceivable ways in which triploidy might have originated, such as the formation of the embryo from a triple fusion endosperm nucleus. This method is improbable, however, for the *Œnothera* embryo-sac only contains four nuclei (two synergids, the egg and a polar nucleus) and there is very little endosperm-formation.

It is highly probable that the exceptional degree of variation in *gigas* is concerned, at least in part, with changes in the chromosome-number of different individuals. A number of these types have been figured (21, 24).

Series of mutations which are parallel to those of *Lamarckiana* have been obtained by Stomps (29) and by Gates (18) in different races of *O. biennis*. Stomps obtained two mutants from the F_2 of *biennis* × *biennis cruciata*. The cruciate variety differs from the normal (from which it has probably originated by a mutation) only in the cruciate character of the flowers. This character behaves as a Mendelian recessive, splitting out in F_2. In the F_2 appeared one *O.* mut. *biennis nanella* (dwarf), and one *O. biennis semigigas* which was larger and possessed twenty-one chromosomes, having also long styles unlike *biennis* races.

In a race of *O. biennis* from the Madrid Botanical Garden, which had evidently undergone crossing (18), many of the plants belonged to types corresponding to *Lamarckiana*, *rubrinervis* and *lævifolia*, while one resembled *gigas* somewhat in foliage, and one was *biennis lata*, having *lata* foliage and no pollen, but with small *biennis* flowers.

Gates (21) has also obtained a dwarf mutant as well as other variations from wild *O. grandiflora* from Alabama. He has also (20) cultivated a race of *O. gigas* identical with that of De Vries, which originated (evidently as a mutation) in the Botanical Garden of Palermo, Italy. This also has twenty-eight chromosomes in typical individuals. Another extensive series of parallel mutations, some of which agree with the De Vriesian forms while others differ widely, has been studied by Heribert-Nilsson (24) in a Swedish race of *O. Lamarckiana* which differs somewhat from the race of De Vries. The giant race in particular is markedly different from the Amsterdam form, though it gives in its progeny one type closely resembling the latter. Of the nine mutant types obtained, only one (*lata*) agreed entirely with the mutants of De Vries.

It is evident, therefore, that the mutation behaviour is by no means confined to *O. Lamarckiana*, but is found in other species as well, races even of *O. grandiflora* showing a certain amount of it when taken immediately from their native wild conditions. Davis (7) has shown that wild *O. grandiflora* contains a number of biotypes. This is, of course, not surprising, for it is clear that many wild species consist of numerous freely intercrossing biotypes. And it has come to be recognized that numerous open-pollinated species are hybrid in the sense that various biotypes have contributed to their ancestry.

The activity in the cytological and experimental study of the Œnotheras has led naturally to a much more critical systematic study of the group, with the result that scores of distinct forms are now being recognized which were formerly classed with such species as *O. biennis* L. or *O. muricata* L. Many of these at least are not merely elementary species in the narrow sense, but forms which stand apart from the described species to a surprising degree.

Among such new species recently described are *O. ornata* and *O. MacBrideæ* of Nelson from Wyoming. These both have larger flowers and longer styles than *O. biennis*, thus forming a transition to the large-flowered species. Bartlett has described *O. Tracyi* from Alabama. This is virtually a small-flowered *O. grandiflora*. Steele has described a new segregate from the *O. biennis* series from Illinois under the name *O. canovirens*. Quite recently a very distinct small-flowered form was described by Gates (19) from Ithaca, New York under the name *O. angustissima*, and Bartlett and Atkinson (3) have characterized two other new forms from the *O. biennis* series of the same locality, under the names *O. nutans* and *O. pycnocarpa*. In another paper (2) Bartlett concludes that the species now commonly naturalized on the dunes of Holland should represent the type of *O. biennis*, and he identifies a paler-flowered race which is now common in Holland and which was formerly known under several pre-Linnæan polynomials, as *O. biennis* var. *sulphurea* De Vries.

The third part of Léveillé's monograph (26) has appeared, but its treatment is not critical and it can be of little benefit in the present intensive study of the genus.

Professor De Vries (13) with Mr. Bartlett made a visit to the type-locality for *O. grandiflora*, in Alabama, last year—the locality where Bartram discovered this species in 1778. They found both *O. grandiflora* and *O. Tracyi*, and a number of races or variations of each. These forms freely intercrossed, at least in the case of *grandiflora*, so that no forms were free from the suspicion of hybridization. This confirms a fact which had already been emphasized by Gates (15), namely, that in open-pollinated plants the intercrossing of many closely-related races which make up the population is continually taking place in every generation. The fact that *O. Lamarckiana* has undergone crossing does not therefore render its condition essentially different from that of any other allogamous species.

Much attention has been devoted to the history not only of *O. Lamarckiana*, but of all the related species in Europe. Many of the early records, from 1614 to the present time, have been brought together by Gates (14), and in this and subsequent papers many of the plants referred to or figured under pre-Linnæan polynomials have been identified with reasonable certainty. The writer's first conclusion, that the original form brought to Europe most resembled *O. Lamarckiana*, has since been modified, but it seems certain that forms agreeing with *O. Lamarckiana* were growing wild in Europe at the time this species was recognized and described from garden material in Paris about 1797.

In drawing any conclusions concerning the origin and history of *O. Lamarckiana*, whether through crossing or otherwise, the following crucial facts must be kept in mind: (i.) That a large-flowered *Œnothera* from "Virginia" was recognized by Ray as early as 1686. This must have belonged to a race either of *O. grandiflora* Solander or *O. Lamarckiana* Ser., and the possibility that it may have been the latter is certainly not excluded. (ii.) Three forms, including (a) *O. biennis* in the general sense, (b) *O. muricata*, and (c) a large-flowered form belonging to *O. grandiflora* or *O. Lamarckiana*, were clearly recognized and figured by Barrelier in 1714; (c.) was probably the same as the large-flowered form of Ray. (iii.) The early synonomy gives clear evidence that this large-flowered form was cultivated in many Botanical Gardens in pre-Linnæan times. (iv.) An *Œnothera* which belongs to *O. Lamarckiana* in the rather narrow sense is now the commonest form in English gardens, where it seeds itself from year to year. (v.) A very similar form has been found by Heribert-Nilsson (24) in the gardens of Southern Sweden. (vi.) A form which is practically identical with that of De Vries has been flourishing in abundance in a naturalized condition on the Lancashire coast since at least 1805.

These facts equally permit two explanations. (a) That *O. Lamarckiana* as it now exists in England, naturalized and in gardens, is essentially the same plant described by Ray and by Barrelier and is descended directly from seeds brought from "Virginia." We now know it to be probable that such seeds would not produce a uniform race to begin with. (b) The other possibility is that the race above-mentioned from Virginia belonged to *O. grandiflora* rather than to *O. Lamarckiana*, the latter originating through crossing afterwards. One weakness of this theory is the fact that *O. biennis* races also occupy this area of Virginia which was first colonized, and that any such crosses would therefore have been repeatedly made there long before the interference of man. Another weakness of this view is that there is no particular reason for supposing that *O. Lamarckiana* characters can be duplicated by single crosses between *biennis* and *grandiflora*, any more than *biennis* could be produced by crosses between *muricata* and *grandiflora*.

It has been suggested by Davis (10) that *O. Lamarckiana* Seringe is only a form of *O. grandiflora* Solander. The suggestion is based chiefly on a comparison of photographs of the type specimens in the Muséum d' Histoire Naturelle in Paris.

The new introduction of *O. grandiflora* from Alabama in 1778 was, no doubt, at least slightly different from the "Virginian *grandiflora*" of Ray and Barrelier, and it appears probable that Seringe meant to express this difference in recognizing *Lamarckiana* as well as *grandiflora*. In any case it is obvious that the question cannot be settled merely by determining the source of De Vries's race of *Lamarckiana* in 1860, for the origin of the much older race of *Lamarckiana* in England must also be considered, and this may easily go back to the time of Ray.

Since it is now clear that numerous races both of *grandiflora* and *Lamarckiana* exist, it seems possible that the original seeds of the large-flowered form brought from "Virginia" contained a mixture of interbreeding races, some of which would now be classed with either species. Certain of the Œnotheras now grown in English gardens might very well represent such intermediate races. Considering the great number of local geographic races of *O. biennis* now being described, it is probably safe to assume that the *grandiflora* of Virginia was different from that of Alabama.

Finally, three of the recent papers have dealt with various general aspects of the mutation problem. These papers are by De Vries (12), Heribert-Nilsson (24) and Gates (21). De Vries reviews the progress which has been made in the study of mutations, particularly in *Œnothera*, and reaffirms his earlier views, such as the premutation theory. He points out that natural selection, mutation and orthogenesis are not mutually exclusive as evolutionary factors, but that all have probably played their part. Heribert-Nilsson contributes a mass of breeding data on a Swedish race of *O. Lamarckiana*, and attempts to explain the mutation phenomena in terms merely of Mendelian splitting. In doing so he disregards the cytological facts and frequently runs counter to them. He elaborates a purely hypothetical theory involving the gradual accumulation of unit-factors or genes in particular germ-cells, but his theory falls to pieces in the light of the cytological facts. As the writer has pointed out, the Mendelian theory of mutation has been disproved and the premutation theory of De Vries rendered unnecessary by the study of the nuclei. The time has come for a new theory of mutation, based on our present cytological and experimental data, and the main achievement of the last three years has been to show that mutation is an independent process requiring a special explanation.

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POSTSCRIPT.

Since this very condensed review was written, an important work by De Vries[1] has appeared, dealing chiefly with *Œnothera* experiments and considering the whole mass of results in relation to the mutation theory. An impression of its comprehensive treatment of the subject of heredity and mutation in *Œnothera* may be obtained from the headings into which the work is divided. These are (i.) the origin of species through mutation, (ii.) reciprocal and double reciprocal hybrids, (iii.) twin hybrids, (iv.) the pangenetic investigation of new species, (v.) the causes of mutations. Many of the results here presented *in extenso* have been published in summary form during the last few years.

The great value of the present book lies not only in the huge accumulation of experimental data which it contains—and this is far more extensive than has ever been brought together for any other similar group of forms—but in the remarkable manner in which the hereditary behaviour and the mutation behaviour are shown to be correlated. The analysis of various wild species, such as *O. biennis* L., *O. muricata* L., *O. Hookeri* Torr. and Gray, *O. cruciata* Nutt., *O. strigosa* Rydb., and several undescribed species, is carried out by means of extensive series of crosses. These are the reciprocal and double reciprocal hybrids. For the most part the reciprocal hybrids are unlike, being usually patroclinous. In this way it is shown that the pollen and egg-cells of various species are carrying different qualities, those of the pollen being usually nearly the same as the external characters of the plant, while those carried by the eggs are quite different and can only be brought to light by crossing with certain species whose pollen and egg-cells carry the same characters.

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[1] De Vries, Hugo. "Gruppenweise Artbildung, unter specieller Berücksichtigung der Gattung *Œnothera*." Gebrüder Borntraeger, Berlin, 1913; pp. 365, with 22 coloured plates and 121 text-figures.

Species which bear the same qualities in both the male and female sex-cells, and whose reciprocal hybrids are therefore alike, are designated *isogamous;* while species whose functional male and female cells are unlike in their latent capacities are called *heterogamous.* Thus *O. Hookeri*, *O. Cockerelli* and *O. strigosa* are found to be isogamous as is also *O. Lamarckiana;* while *O. biennis*, *O. biennis Chicago*, *O. cruciata* and *O. muricata* are heterogamous.

In all these cases there is nothing resembling the Mendelian recombination of many independent characters, but the various hybrids remain constant and uniform in later generations, except in an occasional character such as flower-size. The hybrid types agree in their main essentials for various crosses, and are therefore given names:—*rubiennis*, *conica*, *gracilis*, *rigida*, etc. Thus *O. muricata* × *O. Hookeri*, *O. muricata* × *O. Cockerelli*, *O. Hookeri* × *O. Cockerelli* and *O. Cockerelli* × *O. Hookeri*, etc., all give the *rigida* type, differing from each other only in minor features. By such parallel series of crosses the character of the "Pollenbild" and "Eizellenbild" of each species is determined, and De Vries calls the process *gamolysis.*

Among other cases in which a similar behaviour occurs may be mentioned *O. Hookeri* × *O. biennis*, which gives an F_1 of the *rubiennis* type, the latter splitting in later generations into *rubiennis* and "*Hookeri.*" *O. biennis Chicago* × *O. Hookeri* and *O. cruciata* × *O. Hookeri* give the same result. This is explained by the isogamous condition of *O. Hookeri* and the heterogamy of the other three species. In *O. Hookeri* × *O. biennis*, e.g., the *rubiennis* hybrid bears in its egg cells only the characters of *Hookeri* while the pollen bears the segregated characters of both parents. Hence the type of splitting observed.

Further, not only these crosses but also the twin hybrids (*læta* and *velutina*) and the equally extensive series of mutation crosses (with the mutants), involving yet a third type of hereditary behaviour, are all finally explained and harmonized in connection with the theory of mutation.

De Vries explains not only all this hereditary behaviour but also the mutation phenomena in terms of his hypothesis of intracellular pangenesis. Each pangen represents a special character, and a pangen may be in (i.) the active, (ii.) the inactive, or (iii.) the labile condition, pangens in the labile condition giving rise to mutations. A mutation also consists in the passage of a pangen from one condition to another, or sometimes in the addition of a new pangen. Thus in *O.* mut. *nanella* the pangen for stature has passed from the active to the inactive condition, in *O.* mut. *rubrinervis* this pangen is active, while in *O. Lamarckiana* it is in a labile condition. Hence *Lamarckiana* × *nanella* gives some dwarfs in F_1 while *rubrinervis* × *nanella* yields only talls in F_1 but a varying proportion of dwarfs in F_2.

I have only touched upon a few of the items in this remarkable book, which boldly attempts to explain all the intricate breeding behaviour in *Œnothera.* Though one cannot agree with all its statements, yet the lucid explanations given make the work of great value to all students of heredity and evolution.

One other point to which reference may be made is found in the recent work of Gates and Miss Nesta Thomas. They have not only corroborated the independent results of Miss Lutz and Gates regarding the constancy of the fifteen chromosomes in O. mut. *lata*, but have found the same number constantly in *semilata* and also in two cases in which *lata* foliage, occurring as a mutation, is combined with other characters inherited from the parents.[1]

Thus *O. biennis* mut. *lata* appeared in a race of normal *O. biennis* , having *lata* foliage and *biennis* flowers (15 chromosomes). Again. *O.* mut. *lata rubricalyx* occurred in the F_2 of *O. rubricalyx* × *O. grandiflora*. The great bulk of these plants were blends and combinations of the characters of the parents, but *lata rubricalyx* had *lata* foliage and habit together with the red pigmentation of *rubricalyx*. The possession of fifteen chromosomes by this plant also shows that whenever a meiotic irregularity leads to the formation of an individual having an extra chromosome, such a plant will have the leaves and habit of *lata* or *semilata*.[2] It further shows the sharp contrast which must be drawn between sporadic mutations and the regular processes of inheritance either in pure races or in hybrids.

We may conclude that the work of De Vries and other students of *Œnothera* has resulted in showing that really new characters may and do arise by a germinal change, and are not merely recombinations of the characters of hybrids. The importance of this conclusion is very great at a time when we have been asked to suppose that all evolution has been accomplished by the shuffling and successive loss of fixed Mendelian unit-characters.

REVIEW.

BRITISH VIOLETS:

A monograph, by Mrs. E. S. Gregory; with an introduction by G. Claridge Druce, M.A., F.L.S., Cambridge (W. Heffer & Sons, Ltd.), 1912; pp. xxiii and 108; Price 6*s*. 6*d*.

In this work, the twelve British species of violets are described, including twenty-seven varieties, and numerous hybrids and hybrid-forms. Of the species, three (*V. calcarea*, *V. epipsila*, and *V. montana*) are not to be found in the current British floras. *V. calcarea* is closely allied to *V. hirta*, and was formerly included in *V. hirta* var. *calcarea*. *V. epipsila* is closely allied to *V. palustris*, and is by some botanists considered a variety of it; and *V. montana* is closely allied to *V. ericetorum* (=*V. canina* in Mrs. Gregory's book), and may be a hybrid of *V. ericetorum* and *V. stagnina*.

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[1] Evidence which shows that Mutation and Mendelian splitting are different processes. Section K, British Association, Birmingham.

[2] It is possible that one of two other mutants also have an extra chromosome,

The chief scientific value of Mrs. Gregory's monograph lies in the assistance it affords to students of variation. For example, five varieties and two *formæ* of *V. odorata* are described, and nine varieties and three *formæ* of the allied *V. hirta*. In addition, five hybrid-forms are delineated of the putative hybrid *V. hirta* × *odorata*. One of the latter is referred to *V. collina*, which is usually treated as a distinct species in continental floras.

Botanists of Benthamian leanings will be shocked by such intensive treatment. However, most of the forms described by Mrs. Gregory certainly exist in nature; and the authoress has, in the reviewer's opinion, done a real service in drawing attention to them. Botanists may say, if they choose, that the existence of all these intermediates prove that *V. hirta* and *V. odorata* are only extreme forms of a single species; but this argument, if applied consistently, would result in such a wholesale reduction of species that the followers of Bentham would themselves shrink from accepting their own conclusions. In the present book, intermediates (many of which are most probably of hybrid-origin) are also described between *V. odorata* and *V. hirta*, *V. epipsila* and *V. palustris*, *V. riviniana* and *V. sylvestris* (=*V. reichenbachiana*), *V. ericetorum* and *V. riviniana*, *V. riviniana* and *V. rupestris* (including *V. arenaria*), *V. ericetorum* and *V. stagnina*, *V. ericetorum* and *V. montana*, *V. ericetorum* and *V. lactea*, *V. lactea* and *V. riviniana*, and *V. montana* and *V. stagnina*. Thus, if the existence of intermediates be deemed of sufficient importance to justify the reduction of species, we should be left with only three British violets, one including the present *V. hirta* and *V. odorata*, the second including *V. epipsila* and *V. hirta*, and the third including all the caulescent forms. This indeed would represent Bentham's views of the British violets, except that he retained *V. hirta* and *V. odorata* as distinct species, and that in a late edition of his *Handbook*, he added *V. arenaria* as a distinct species. One unfortunate effect which the synthetic grouping of allied plants into aggregate species undoubtedly has is the obscuring the important biological fact that the majority of the smaller species remain distinct and without intermediates wherever they grow apart from their allies. Thus *V. riviniana* on the siliceous soils of the Pennines shows no signs of approaching *V. sylvestris*; but in the woods on calcareous soils in southern England where both plants occur, it is not difficult to connect the two forms by a string of intermediate plants. Such facts—and they are commoner than botanists have been inclined to believe—suggest that the two very different phenomena of hybridisation and variation have been confused by botanists of the Victorian period. Doubtless the two phenomena are, from some points of view, very closely related; but it seems obvious that, from other points of view, they must be kept separate and distinct. Mrs. Gregory's book is valuable because it honestly makes the attempt to keep the two phenomena distinct; and it succeeds in this as well as any attempt which is not based on actual experimental work can succeed.

Here it may be pointed out that the actual crossing of British violets is no easy task on account of the small size of the flowers; but, as cleistogamous flowers are of common occurrence, it should be a simple matter to obtain self-fertilised seeds of the putative hybrids. These seeds should be sown with a view of ascertaining whether or not the parental characters segregate in some Mendelian manner, since, if they do, the existence of hybrids in the genus would be established. It should, of course, be remembered, that the starting point would almost certainly not be an F_1 plant, but a segregate whose precise parentage is unknown. If Mrs. Gregory's work on British violets leads to some such experimental work it will not have been labour in vain.

There are one or two matters in connection with the book with regard to which we confess to a little disappointment. The geographical distribution of the species and varieties outside the British Isles is not given; and even their British distribution is given inadequately. Again there are neither diagnoses of the sub-generic divisions nor artificial keys to the species; and hence it is difficult to make full use of Mrs. Gregory's careful descriptions of the species and lower forms. *V. sylvestris* var. *punctata* (p. 39) cannot be a "comb. nov." if it is correctly attributed to Druce in Hayward's *Bot. Pocket Book*: in any case, however, this varietal name is probably incorrect.

Apart, however, from these minor blemishes, the book is without doubt a real contribution to science; and Mrs. Gregory may be heartily and sincerely congratulated on the general result. The book contains illustrations of most of the species and of several of the lower forms. The printing is very good; and the general appearance of the book is very clean and neat: a word of praise is therefore due to Messrs. Heffer, the printers and publishers.

Mr. Druce's introduction gives a useful synopsis of the history of the study of British violets from the 16th century to the present time.

Perhaps it may be well to explain that "violets" are the members of the section *Nominium* of the genus *Viola*, and that "pansies" (such as *Viola tricolor* and *V. lutea*), which belong to the section *Grammionium*, are not dealt with in the book.

C. E. M.

THE

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THE HISTOLOGY OF THE CALLUS TISSUE IN *ALTHÆA ROSEA.*

BY WINIFRED BLACKWELL,
Imperial College of Science and Technology.

[WITH ONE FIGURE IN THE TEXT.]

IT is well known that typical wound callus tissue is formed by the renewed growth of certain living cells in the neighbourhood of the wound, in a direction perpendicular to the surface of the wound. Subsequently, repeated tangential walls are laid down, so that elongated cell rows are formed, which later fuse, probably by the softening and partial hydrolysis of their walls, to form a pseudoparenchymatous tissue, in which further differentiation may or may not occur, although the outer edge of the tissue becomes constantly suberised.

In the course of an investigation on wound reactions in the pith of *Althæa rosea*, a stage in callus formation was found, in which, owing to the weakness of the wound stimulus, cells here and there had grown to form rows, without lateral fusion. Careful examination revealed the fact that the outer surface of the wall of these cells was not smooth but was studded with minute outgrowths in the form of short rods or stalked spherical heads (Fig. 1), obviously of secondary formation and of different substance, since they remained uncoloured with chlor-zinc-iodine in contradistinction to the rest of the wall which became violet. Küster has described this warted condition of the wall as characteristic of young callus tissue, and it is also interesting to note that Mangin has found analogous structures very frequently on the walls lining the intercellular spaces of plants. They therefore appear to be characteristic of the walls of cells not normally exposed. In spite of the frequency of the occurrence of these papillæ, investigations as to the nature of their substance have led to rather conflicting results. They have been called mucilaginous (Noack), protoplasmic, cuticularised (Luerssen, Mellinck), or related to cutin (Jost), and finally Mangin has shewn convincingly that in intercellular spaces the papillæ most often consist of calcium pectate.

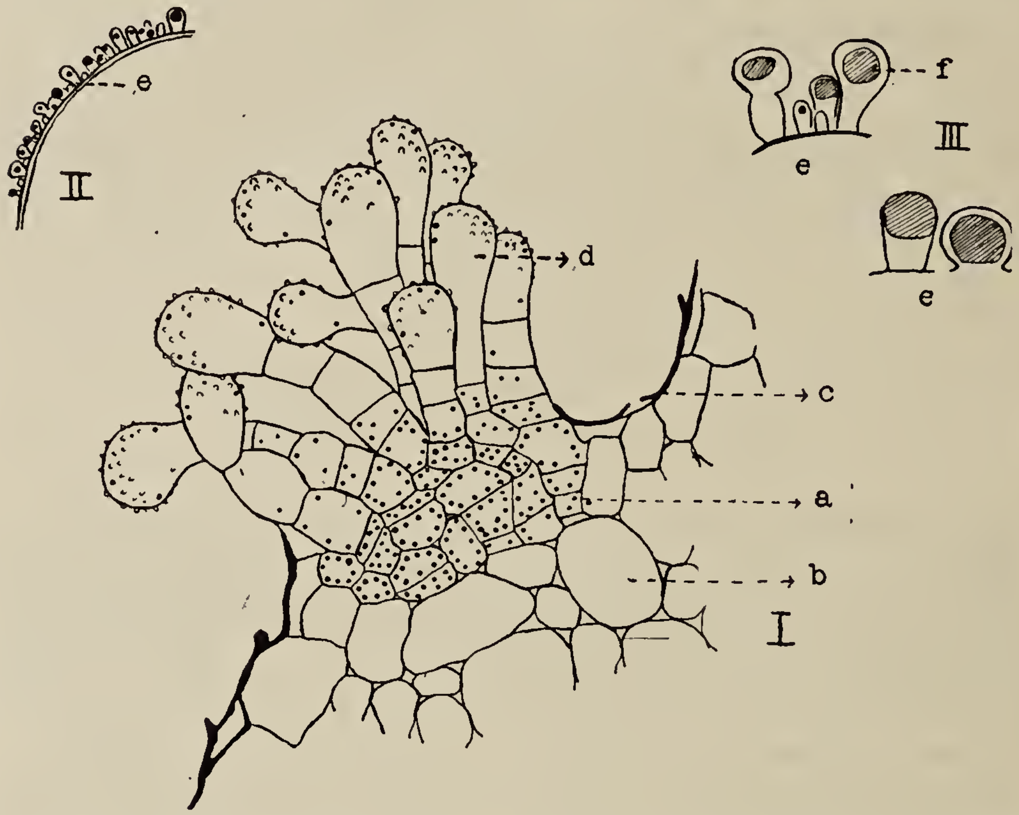

Fig. 1. Callus in *Althæa rosea*. I. Wound callus tissue arising from pith. II. Wall of callus cell showing papillæ (stained with iodine). III. Papillæ very highly magnified. Lettering:—*a*, meristematic zone with much starch; *b*, normal pith cells; *c*, thickened walls of collapsed pith cells at wound surface; *d*, hypertrophied callus cells with papillate walls; *e*, papillæ; *f*, central spot stained blue with iodine.

It was thought worth while to investigate, micro-chemically, the papillæ on the callus walls of *Althæa*, to see if the nature of their substance could be determined, and hence, to find an explanation for the discrepancies in accounts of those who have formerly observed them. Micro-chemical investigations were made difficult by the exceedingly small size of the papillæ, but by repeating each test several times, and by examining under a $\frac{1}{12}''$ objective in doubtful cases, some results were obtained which may be regarded as accurate.

The reactions given in *Althæa* differ from any as yet reported. Some of these differences may be correlated with the fact that the material examined had been preserved for a considerable time in alcohol; the varying results obtained by different authors make it more probable that the substance of the papillæ is really variable. So far two main views have been held as to the nature of the substance in question. It has been stated both to be cuticular and pectic. The reactions given by the papillæ in *Althæa* were certainly typical of neither substance.

On staining with iodine, two regions could be distinguished in the larger papillæ: a central blue spot and a colourless surrounding layer continuous with the stalk. The central spot gives all the reactions characteristic of the cell walls of *Tropæolum* seeds and one may therefore perhaps assume that it consists of hydrated cellulose or amyloid. The papillæ are thus not homogeneous in structure, as has been asserted. The fact that they exhibit this differentiation may throw some light on their mode of origin. The substance of the outer part of the papilla and of the stalk is more difficult to identify. It is typically neither cutin nor pectin. Although it shews points of resemblance to both, micro-chemical tests only serve to exclude it from identity with any of the usual constituents of the cell-wall. Thus, the substance remains uncoloured with all iodine reagents, so that cellulose is absent. Recognised tests for mucilage and callose fail. There is no evidence of the presence of lignin. Almost every recognised test for pectic substances was tried, without success. In spite of the failure of the usual tests, the fact that the papillæ underwent considerable swelling with reagents such as calcium chloride, potash and ammonia, coupled with Mangin's very definite proofs of the presence of pectic bodies in the papillæ of intercellular spaces and, in addition, the recognition of the large percentage of pectic substances present in the cell-walls of the normal pith, made it difficult to abandon entirely the idea that the substance in question was a modification of a pectic body. One fact supported this view. The papillæ were not dissolved by dilute potash after treatment with concentrated hydrochloric acid and alcohol (1 : 3) for twenty-four hours, as is the case with ordinary pectic bodies. If, however, sections were placed in potassium chlorate and hydrochloric acid for a few hours, and then irrigated with dilute potash, not only did the cells fall apart owing to the solution of the pectic bodies, but the papillæ disappeared instantaneously. We may be dealing here with a hydrolysed product of a pectic body, the latter being reconstructed under the oxidising action of the chlorate.

Similarly, although most of the tests for cuticular substances failed, there were a few reactions indicating that the substance in question is related to cutin. With Schulze's macerating solution, and again with 25% chromic acid, the papillæ separated from the membrane, but were not completely dissolved. Small rings and ellipses, representing the more or less spherical heads of the papillæ after solution of their central spot remained floating in the solution. With iodine followed by concentrated sulphuric acid, the papillæ turn brown without swelling, and again become separated from the membrane. A less resistant basal zone may possibly be present. It is interesting to note that by adjusting the concentration of the acid, the callus cells may be made to shrink, leaving behind, as they do so, a very fine colourless membrane to which the papillæ are attached. In one case a thin brown cap, studded with papillæ, floated off from the apical cell of the callus row. The degree of resistance of the papillæ to chromic and sulphuric acids is similar to that offered by cuticular substances, but whether this is an adequate reason for relating their substance to cutin is somewhat doubtful. The identification of the substance with a hydrolysed product of pectic acid is based on more convincing evidence, and its resistance to acids, in this case, may possibly be explained by the circumstance that a pectic mucilage on exposure to air is apt to become altered into a tough horny substance of unknown composition. If this is so, the outer walls of the callus cells may have undergone partial hydrolysis and softening in preparation for subsequent fusion. The cellulose constituent has become amyloid, the pectic bodies have been hydrolysed to pectic mucilages. Since in this case fusion has not occurred between neighbouring cell rows, the hydrolysed products have become hardened on exposure to the air and have formed a resistant layer around the cells. It may be noted in this connection that Mangin, when working on similar protuberances in the intercellular spaces of plants, found reasons for regarding them as pectic in nature. We may perhaps correlate them with the fact that the air in the intercellular spaces is not rapidly renewed, and therefore the hardening process has not occurred.

So far we have assumed that the resemblance of the unknown substance to cutin is accidental, and based only on its resistance to certain reagents. We have to face the possibility that the resemblance to cutin is actual and indicative of relationship. If this is the case, how has cutin been laid down in the papillæ? It was certainly not present, as such, in the walls of the original pith-cells. Although we know nothing certainly of the mode of origin of cutin in walls, it may be suggested that it has originated by the transformation of one of the known constituents of the wall. The young cell-walls of a typical plant consist of pectic and cellulose bodies. Where these are exposed—*e.g.*, epidermal cells, walls of pollen-grains, etc.—cuticularisation frequently occurs. Mangin noticed that in the walls of Fungi where pectic bodies were constantly absent, cuticularisation never occurred; from this fact, supported by many other observations—*e.g.* the tendency of pectic substance to accumulate on the outside of the cell—Mangin was led to suggest that cutin was formed by the transformation of the pectic constituents of the wall. This seems a possible explanation of the present difficulties. If the hypothesis is correct, we are dealing with different transition stages in a series of plastic substances in which pectic bodies and cutin are the first and last terms. The composition of the wall is determined by the degree of exposure to the air. Middle lamellæ are therefore definitely pectic in nature. The walls lining intercellular spaces, whether papillæ are present or not, are generally pectic, although they give cuticular reactions in some cases, especially when the spaces are large, as in the Nymphæaceæ; (cf. also Jost on papillæ of the intercellular spaces of the pneumatophores of *Phœnix*). The papillæ on the walls exposed by wounding are more definitely related to cutin. The outer walls of epidermal cells are typically cuticular.

Since the pectic substance of the middle lamella is chiefly in the form of calcium pectate, if cutin be the final product of its transformation, calcium must necessarily be expelled at some stage, It is of interest to note that a large number of calcium oxalate crystals are present both within the cells of the callus-tissue and on the tips of the cell-rows. Comparison may be made with the leaves of such a plant as *Ficus*, the epidermis of which is characterised by a thick cuticle, and by the localisation of special calcium carbonate reserve cells among the normal ones.

It is difficult to see of what use to the plant the papillæ of the intercellular spaces may be. Mangin has suggested that their significance is not teleological, but depends on a purely mechanical flowing together into little lumps of the partially lignified substance of the middle lamella in the formation of the intercellular spaces. Similarly, the papillæ on the walls of callus cells may be formed mechanically during the softening of the walls prior to fusion, the hydrolysed pectic substance collecting, as is usual, towards the outside of the wall. Where fusion of the cell-rows has not occurred, the pectic substance on exposure to the air has undergone "hardening." Where a parenchyma has been formed, only the original end walls of the cell-rows remain exposed. They were formerly characterised by the presence of a very large number of pectic outgrowths. After the fusion of the rows, they are characterised by a thick cuticular outer membrane, and therefore form a resistant edge to the callus-tissue.

In *Althæa*, therefore, we have additional evidence supporting Mangin's hypothesis as to the mode of origin of cutin. The two essential processes are (i.) the accumulation of the pectic bodies in the outer layers of the wall; (ii.) the transformation of the pectic bodies on exposure, (*a*) into pectic mucilages with increase of volume, (*b*) into cutin, a "hardening" process involving the expulsion of calcium.

I wish to acknowledge the kindness and help I have received from Professor J. B. Farmer, F.R.S., in connexion with the present research, which was done during my tenure of a London County Council Research Scholarship at the Imperial College of Science.

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ON THE VASCULAR ANATOMY OF THE RHIZOME OF *PLATYCERIUM.*

By Harriet E. Allison, B.Sc.,
Carnegie Research Scholar, Glasgow University.

[With Five Figures in the Text].

WHEN this investigation of *Platycerium* was begun, it was not anticipated that the vascular anatomy would show such complexity of structure as now appears. The axis of the fern is much abbreviated, and the stelar structure much divided, forming an anastomosing network. The leaves, which are of two kinds, are so closely arranged on the axis that before one leaf-trace is clear of the axial system, another is being given off from it. Moveover, it was found that a medullary system was present in the more complex cases. I have worked through several species of the genus, both in the old and young condition. But though the results may have their value ultimately as helping to define the position of *Platycerium* among the Ferns, they do not supply any readily appreciated or immediately distinctive points. I shall, however, attempt at the close to indicate along what lines the relationships of *Platycerium* may be found.

Platycerium alcicorne Desv. is one of the smaller forms of the genus. The rhizome is dorsiventral, with leaves inserted on the upper surface, and the lower surface covered with dark wiry rootlets. The leaves, which are of two kinds, the nest-leaves and

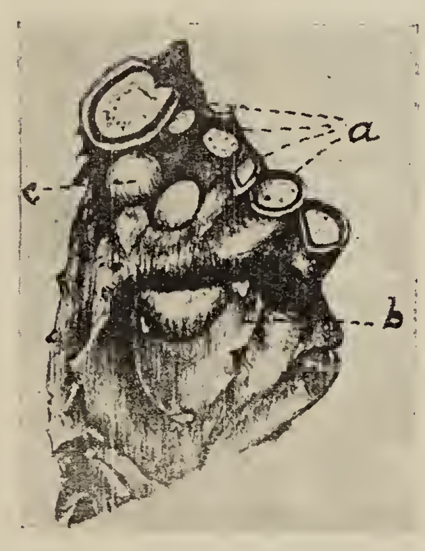

Fig. 1.—*Platycerium alcicorne.* Side view of rhizome: *a*, foliage-leaves; *b*, nest-leaves; *c*, vegetative bud.

the foliage-leaves, are inserted in two rows upon the axis, a series of nest-leaves alternating with a series of foliage-leaves. Fig. 1, a side view of the rhizome of *P. alcicorne*, shows the leaf bases of a series of foliage-leaves, and also the bases of the decayed nest-leaves, which closely invest the axis and act as a protection for the younger leaves. On the ventral surface, the dark covering of rootlets was removed in order to show the vegetative buds, which arise at the bases of the leaves as brown swellings.

The young plant of *P. alcicorne* shows a condition more nearly approaching the simple dictyostelic types of fern than any of the other specimens examined. The plant described was a small tuberous one about 3 mm. in diameter, and serial sections were cut through several leaf bases up to the apex. The apex is protected by hard brittle hairs, which have become expanded into elongated scales. These scales consist of two rows of cells, with a hard brown substance between, which extends the length of the scale. In this plant, one leaf had expanded and the petiole has a ring of five or six vascular bundles, embedded in a ground-mass of parenchyma. Surrounding these strands is a ring of smaller, sharp-angled cells, which show slight thickening on the walls and later form a band of sclerenchyma, external to the narrow-celled endodermis.

The relation of the leaf-trace to the vascular system of the axis is simpler and more easily understood than in the older plant. The whole rhizome is covered with elongated scales, and on the ventral surface rootlets pursue an oblique course through the cortex. The ground-mass of the axis consists of thin-walled parenchymatous cells, but here and there thickenings on the cell-wall forecast the sclerenchymatous ground-mass of the mature plant. The vascular system of the axis is a dictyostele consisting of eight or nine meristeles, which anastomose frequently. On the inner face of each meristele a cap of sclerenchyma is found. The leaf-trace, which in the petiole becomes a ring of six vascular bundles, consists, at first, of two strands only (Fig. 2, *4*). One of these meristeles divides into two strands, from which the vascular system of the vegetative bud at the base of each leaf is derived (Fig. 2, *6-10*). Meantime, the adjoining strands of the dictyostele extend across the leaf-gap, and form a commissure (Fig. 2, *9*, *10*). This commissure is temporary, however, and almost immediately divides to form two more strands of the leaf-trace. The leaf-gap is practically closed by a long meristele. At this point the leaf-trace is composed of four strands, which increase by division in the petiole. In the younger leaf, the temporary commissure begins to appear, but never becomes complete (Fig. 2, *18*).

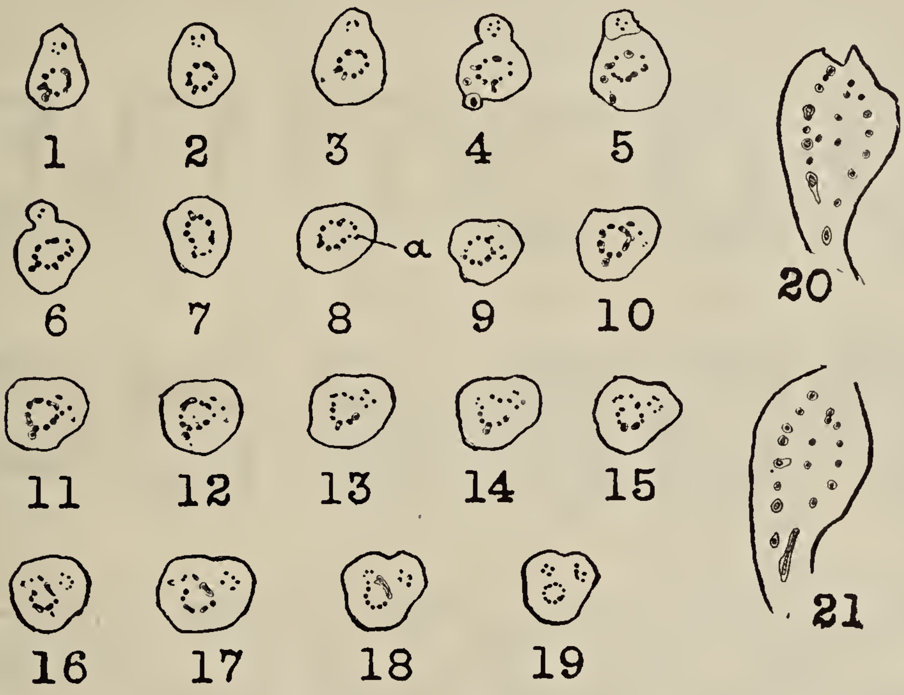

Fig. 2.—*Platycerium alcicorne* (1-19) and *P. æthiopicum* (20-21). 1-19 a series of transverse sections of a young plant of *P. alcicorne*, arranged from below upwards, showing formation of leaf-trace (1-9), formation of vegetative bud (6-10), and petiole of leaf (10-19); *a*, Vascular strands of vegetative bud. 20, 21, Transverse sections of base of petiole of *P. æthiopicum*.

In an older plant of *P. alcicorne* (Fig. 3), it is more readily seen that the vascular system is a "perforated" dictyostele, consisting of a ring of meristeles, which are much subdivided, and form an anastomosing network. On the dorsal surface of the rhizome, the leaves come off right and left, while the whole ventral surface has a thick covering of rootlets, which are given off from the ventral meristeles and traverse the cortex obliquely. A thick ring of sclerenchyma surrounds the vascular system, and the rootlets break through this and are distinguished in the cortex by a dark band surrounding them. The ring of sclerenchyma does not border directly on the epidermis, but is separated from it by some layers of thin-walled parenchyma. The meristeles themselves are simple in structure, consisting of xylem intermixed with parenchymatous cells, surrounded by phloem and pericycle. Outside the endodermis is a sheath of sclerenchyma.

In the series of sections which I have figured, and shall describe, the plant of *P. alcicorne* was almost full grown. The sections were cut through the bases of three foliage-leaves. The leaves are crowded upon the axis and each leaf-trace remains, relatively, a long time in the axis before turning into the petiole. In Fig. 3, *1-7*, the leaf-trace of a leaf (No. 1) has been completely formed, and is seen to consist of a number of strands, which appear to be irregularly disposed in a circle. The course of the

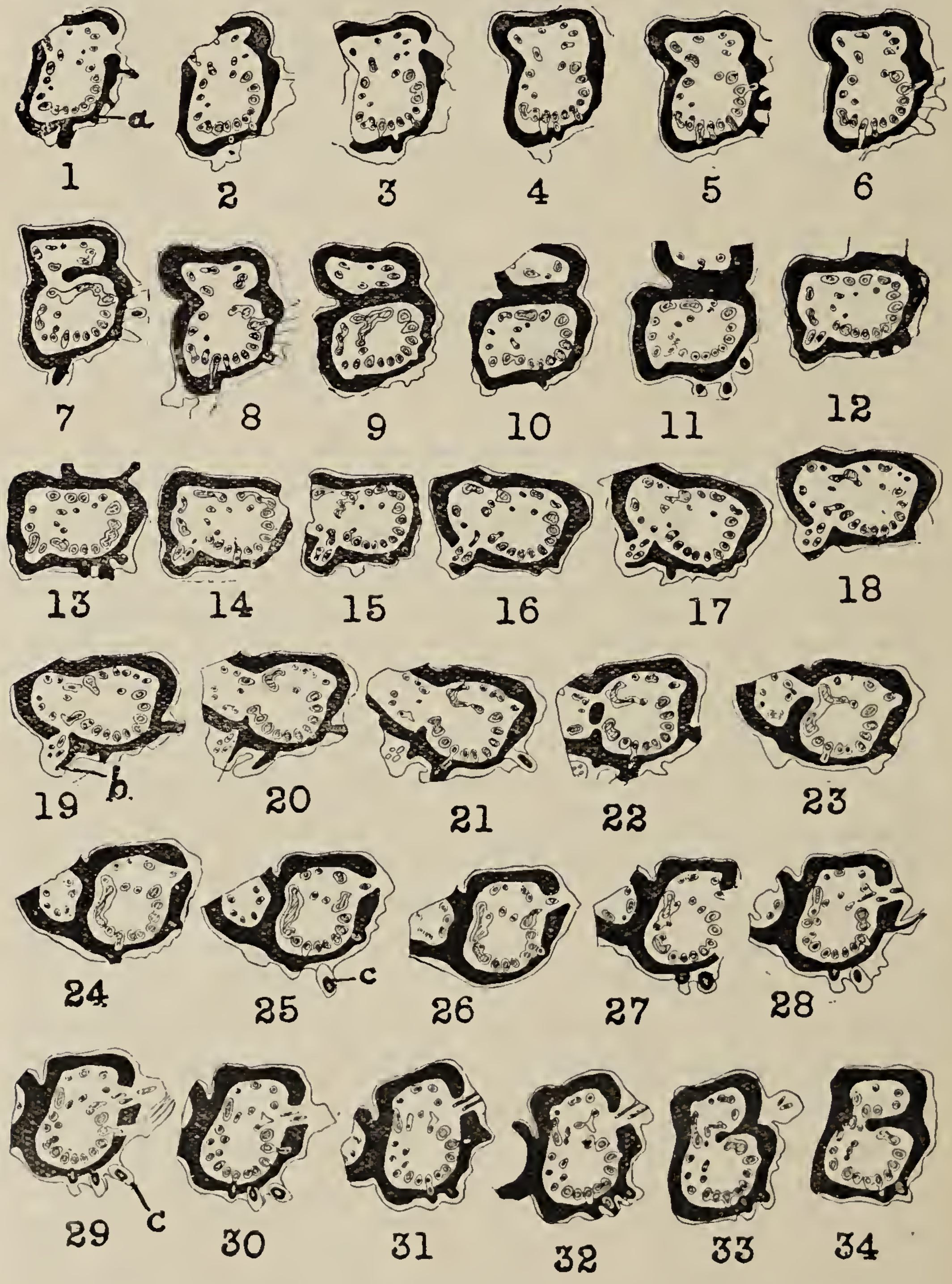

Fig. 3. *Platycerium alcicorne.* A series of transverse sections of the rhizome, arranged from below upwards; 1-11 show leaf-base (No. 1) and formation of leaf-trace of the succeding leaf; 11-24 show formation of leaf-trace and leaf-base (No. 2); *a*, external ring of sclerenchyma (seen in all the sections); *b*, vegetative bud at base of leaf; *c*, rootlets surrounded by sclerenchyma.

leaf-trace in the axis and its origin may be followed for the succeeding leaf (No. 2), which is inserted on the left of the axis (Fig. 3,*1-24*). Thus, in Fig. 3, *1-10*, only changes preliminary to the separation of the leaf-trace are observable; in Fig. 3, *10-20*, the leaf-trace (No. 2) is in course of separation. Before the leaf-trace (No. 1) is cut off from the axis, one of the meristeles on the left divides into two, an internal and an external strand (Fig. 3, *1*). This internal strand persists across the front of the leaf-trace, which appears as a ring of strands (Fig. 3, *1-6*). The leaf-gap of the leaf (No. 1) has been filled by a long meristele, which also takes part in the formation of the leaf-trace on the left (Fig. 3, *8-10*). The trace on the left (No. 2), at this point, begins to move out from the axis and the vegetative bud at the base of the leaf is formed from it (Fig. 3, *11-19*). The sclerenchyma, meantime, forms a little pocket, and two of the strands give off the vascular supply to the bud, which passes into the pocket and is directed obliquely downwards. In Fig. 3, *11*, *12*, one of the meristeles on the right has divided to form the internal bundle of the still younger leaf (No. 3). Fig. 3, *20*, *21*, shows the leaf-trace on the left completely formed, but still remaining in communication with the main axis. An intrusion of sclerenchyma cuts off the leaf-trace finally, and the gap, as before, is filled by a meristele which appears long, since its course lies in the plane of transverse section. In the petiole, the number of strands in the circle increases by frequent division. An examination of the whole series of transverse sections shown in Fig 3, indicates that the origin of the leaf-trace thus described, is repeated for successive leaves.

The anatomy of *P. Willinckii*, Moore, is like that of *P. alcicorne.*

Platycerium æthiopicum is one of the largest forms in the genus. The leaves, which are very large, about 1½ feet long, are of two kinds as in the other species, nest-leaves and foliage-leaves. The foliage-leaves are again divided into sterile and fertile leaves, the latter showing broad soral patches on the leaf expansions and also in the hollows between the expansions. The nest-leaves are large, deep brown when old, and show very distinctly the octagonal veining characteristic of the genus. The rhizome, which is ascending, is practically hidden by the nest and other leaf bases. It is extremely hard, due to the presence of much sclerenchymatous tissue. On the dorsal surface of the rhizome, the leaves are inserted in two alternating rows. After a set of nest-leaves has been formed, the foliage-leaves arise, probably forming a protection for the younger leaves. As the apex of the fern continues to grow, the nest leaves die down, forming a great mass of humus and a number of foliage-leaves succeed them and so on. It is thus seen that the rhizome shows on the dorsal surface two rows of leaves, with a set of nest-leaves alternating with a set of foliage-leaves. On the ventral surface of the rhizome there is a thick covering of dark wiry rootlets.

This species, which is conspicuous in the genus for its large size, shows a corresponding complexity of internal structure. The actual rhizome, the structure of which is about to be described, was one of medium size, measuring about ½ inch in diameter. Serial sections were cut through the insertion of three leaf bases, two of the leaves being foliage-leaves and the other a nest-leaf. The nest-leaf corresponds in essentials to the other leaves, the anatomy and insertion of the leaf being almost similar to that of the foliage-leaves. The form of the nest-leaf would thus appear to be an adaptation to habit, and it seems probable that the nest-leaf and the foliage-leaf originated from a common type.

In transverse section, the anatomy of the rhizome is seen to be somewhat complex. The meristeles are very numerous, and are scattered over the transverse section. Moreover, the close insertion of the leaves upon the axis adds to the complication. It is possible, however, to identify an outer ring of meristeles, forming a dictyostele. These meristeles are seen in the serial sections to unite frequently with one another, and as frequently to divide, so that they form a vascular network. The meshes of this net are not leaf-gaps, but are of the nature of stelar "perforations." Internal to the perforated dictyostele is a large number of medullary strands, which are formed either by division from the meristeles of the primitive dictyostele, or from already existing medullary strands. On the ventral or lower surface, rootlets are given off from the dictyostele as in other species. The whole ground-mass of the rhizome consists of cells with thickened membranes. The meristeles are each surrounded by a sheath of two or three rows of cells with thickly lignified walls. The structure of the meristele is quite normal, and there is no marked protoxylem distinguishable. At the centre is a core of xylem, composed of tracheids with one or two parenchymatous cells, surrounded by a ring of phloem, and by a pericycle two or three cells deep. An endodermis is present, but owing to the hardness of the sheath, it was often crushed or ruptured in cutting.

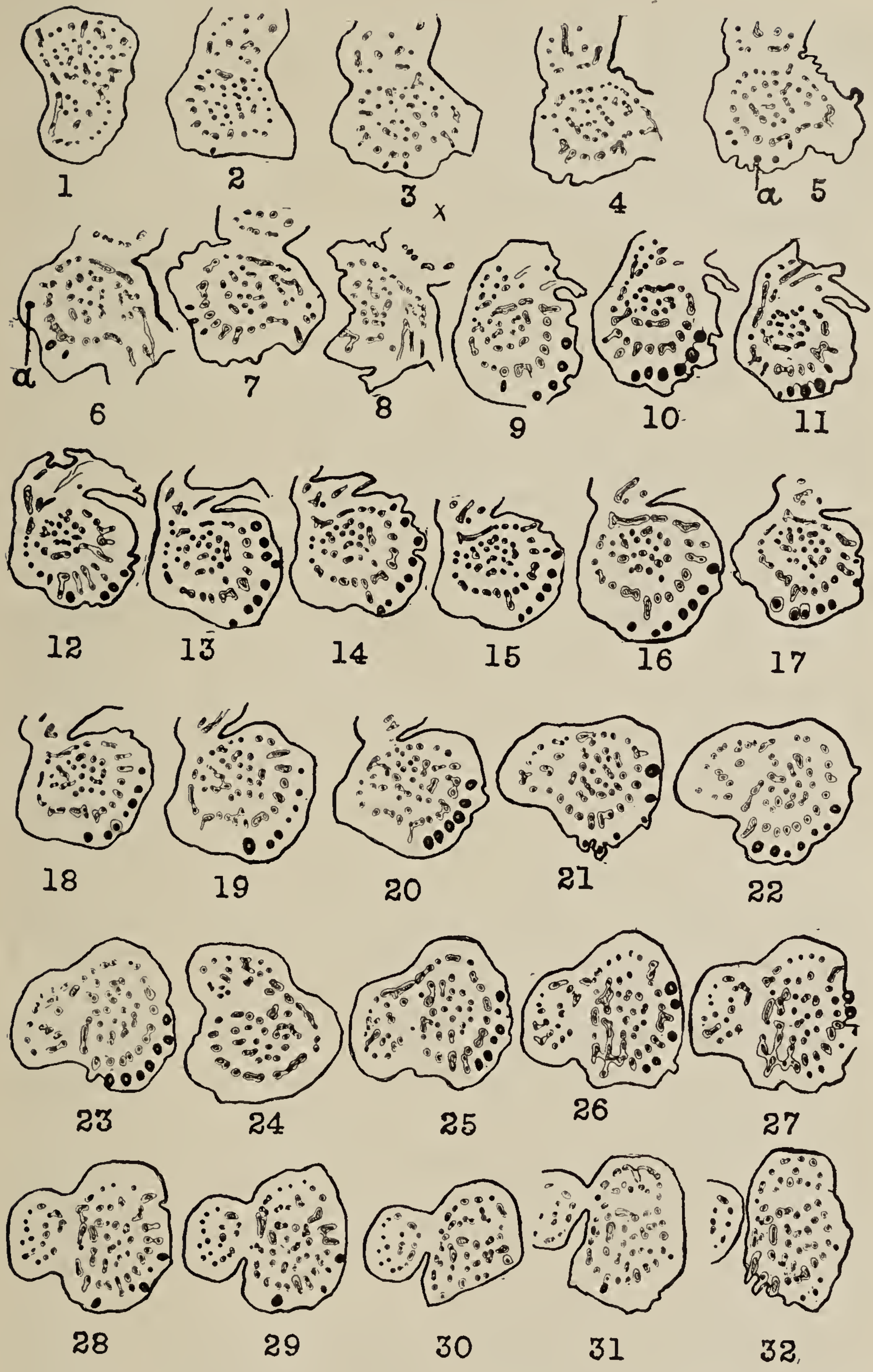

Fig. 4.—*Platycerium æthiopicum.* A series of transverse sections of the rhizome arranged from below upwards: 1-20 show base of nest-leaf; 18-32 show formation of leaf-trace of foliage-leaf; 26 shows base of petiole of foliage-leaf; *a*, rootlets surrounded by sclerenchyma.

In arranging the figures, the orientation of the members of the series has not been strictly maintained; e.g. No. 24 is rotated 90°, and Nos. 4 and 5 have been transposed.

In order to study the relations of the leaf-trace to the vascular system of the axis, serial sections were cut through the insertion of three leaf-bases, two being foliage and the other a nest-leaf. The lowest of the three leaf-traces proved to be that of a nest-leaf (Fig. 4, *1-20*). Preparations for the formation of the leaf-trace in the axis are seen in the expansion of the dictyostele by division and elongation of the meristeles to form a kind of pocket (Fig. 4, *2*). Gradually the dictyostele widens, the strands elongate and finally divide into several strands, which form the outer ring of bundles in the petiole. While this gradual expansion has been taking place in the outer ring, some of the medullary bundles opposite the departing leaf-trace have divided, and these go out as the internal bundles of the leaf-trace. As in the axis, some of the internal accessory bundles are formed by splitting off from the outer bundles (Fig. 4, *6*, *7*). The leaf-trace is now complete and passes out into the nest-leaf, the short petiole showing an external ring of strands and a small number of internal strands. As this kind of leaf is almost sessile, the bundles on the outside of the petiole extend very soon by division or elongation into the expansion of the leaf. The leaf-gap is closed by the elongation of one or two of the accessory bundles to form a transverse commissure (Fig. 4, *15-17*). This is comparable with what is seen in the solenostele of *Acrostichum aureum* (Thomas, 11; Tansley, 10), and also in the dictyostele of *Angiopteris evecta* (Shove, 9), where the gaps are filled by medullary bundles. For some time one side of the leaf-trace remains connected with the main dictyostele, a condition not unusual in dorsiventral shoots of ferns.

When this commissure is formed across the leaf-gap of the next leaf, the dictyostele shows signs of preparation for giving off another leaf-trace (Fig. 4, *17-32*). As in the case of the nest-leaf, the meristeles in that region begin to divide and the whole ring expands. The internal bundles also become more numerous and pass into the gap left by the enlarging dictyostele (Fig. 4, *18-21*). Thus a pocket is formed with a ring of almost equidistant strands on the outside, while internally, in this case, there are three accessory strands, which divide to form the medullary bundles of the petiole. Soon the pocket becomes constricted by an intrusion of sclerenchyma, which takes place from one side only, the other side remaining connected as in the nest-leaf. Finally, when the constriction is complete, the outer strands of the trace divide and thus complete the outer ring of petiolar strands (Fig. 4, *26-33*).

In the leaf-trace, the outer ring of strands is derived from the dictyostele of the axis, while the medullary strands in the petiole arise either from the medullary strands of the axis or by splitting off from the outer petiolar ring. As before, a meristele closes the gap.

In a young plant of this species, there appeared in the earliest stage to be one strand with a core of xylem and parenchyma, a haplostele, surrounded by phloem and pericycle. Very soon, however, phloem and parenchyma appear internally and the original strand is cut into two meristeles by an intrusion of sclerenchyma, of which the ground-mass of the axis is composed. These two meristeles almost immediately divide again, so that four meristeles are present of practically the same nature as those in the mature plant (Fig. 5, *1-4*). The solenostelic stage appears to be omitted. Two of the meristeles unite to form a long dorsal meristele, which persists for some time but later splits into a number of meristeles. The meristeles are constantly uniting and dividing so that the identity of one is not maintained for any length of time. The first indication of the accessory medullary strands, such as are found in the older stem, is seen in the splitting of a small bundle from one of the meristeles (Fig. 5, *11-13*). This little strand remains independent for a very short time and soon joins a neighbouring meristele, only to break away again later as an internal strand (Fig. 5, *14-17*).

The leaf-trace has its origin in one meristele which soon divides into two strands, one of which sub-divides into two immediately (Fig. 5, *17-20*). However, one of these strands joins one of the meristeles of the stem, and the leaf-trace really consists of two strands only, which divide to form the three bundles of the petiole (Fig. 5, *20-24*). After this leaf-trace has been given off, one of the outer meristeles divides into two and the first permanent medullary bundle is formed (Fig. 5, *25*). This bundle, with two other bundles which have split off from the outer ring, form an internal ring (Fig. 5, *26-28*). As in the older plant, these inner bundles unite with each other and also with the outer meristeles. The leaf-trace of the next leaf appears to be formed by two of the outer meristeles, which elongate and extend into the leaf. One of the medullary strands unites with the outer ring and passes into the petiole (Fig. 5, *30-34*).

It is difficult to make a summary of these results, since the structure, particularly in the matter of the behaviour of the medullary bundles is somewhat exceptional. It is to be noticed that in the genus *Platycerium* there is a progression from a comparatively simple type to a more complicated one. In *P. alcicorne* and *P. Willinckii*, the vascular system is a much perforated dictyostele, while in the large species, *P. æthiopicum*, medullary strands are formed as well as the external ring of meristeles. It may be noticed, however, that in *P. alcicorne*, the small bundle is actually an accessory medullary strand and may so far be held as some indication of the more complex state in *P. æthiopicum.* In all the species examined, the leaf-trace takes its origin from more than one strand and the leaf-gap is closed by a long commissure. In *P. æthiopicum*, it is established that the

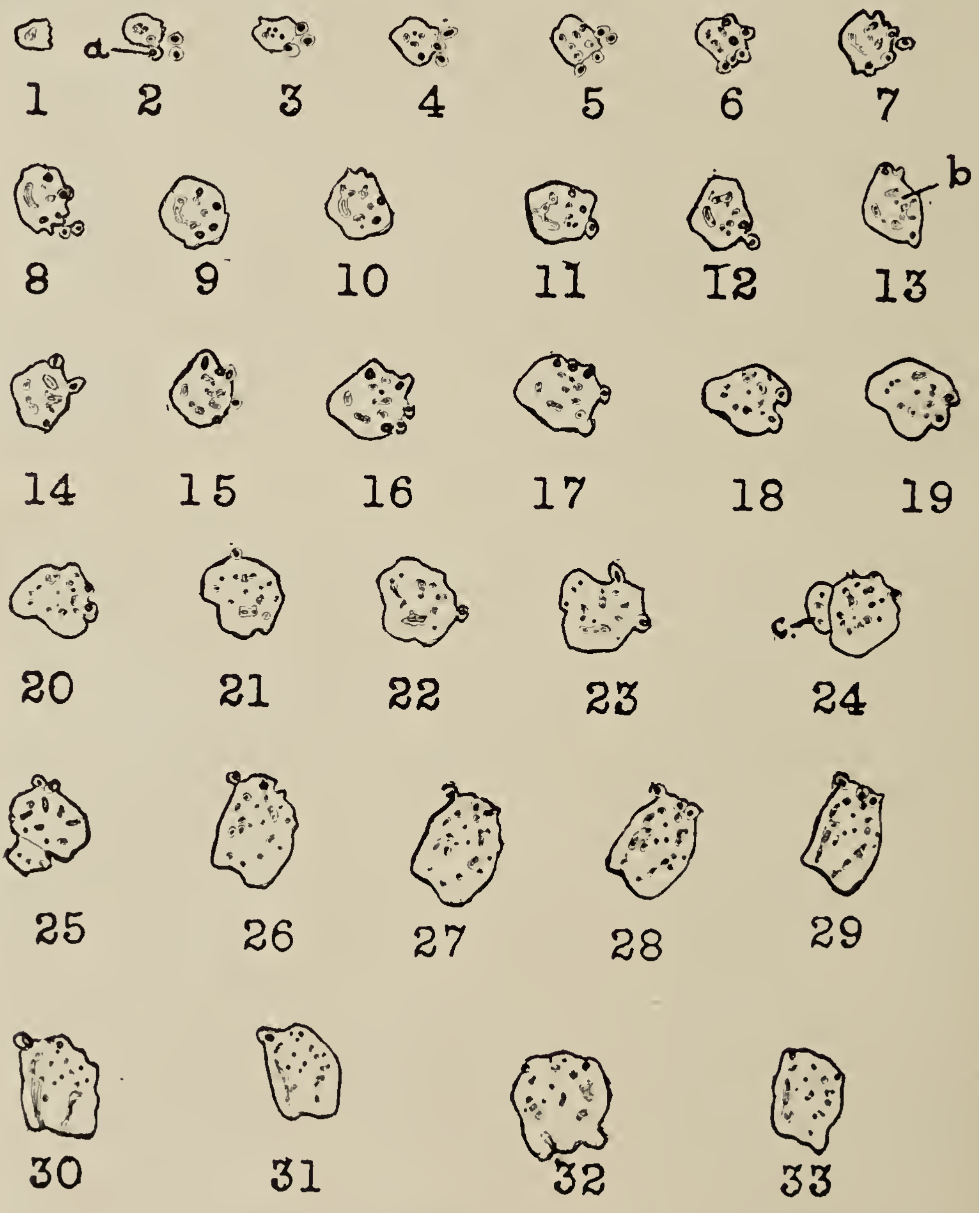

Fig. 5. *Platycerium æthiopicum.* Series of transverse sections of the rhizome of a young plant: 1 and 2 show formation of the dictyostele; 12–14 show first temporary accessory bundle *(b)*; 16–24 show formation of the leaf-trace of the first leaf; 25–34 show formation of leaf-trace of second leaf *a*, rootlets with a ring of sclerenchyma; *c*, base of petiole of the first leaf.

accessory medullary strands arise from the original dictyostele and that in the leaf-trace of the youngest leaf, no accessory bundles are present. Also the medullary strands close the leaf-gap and even the simple accessory strand in *P. alcicorne* (Fig. 3, *1-6*) helps to do so.

As regards the position of *Platycerium* among the Ferns, its vascular anatomy suggests a comparison with the Marattiaceæ and the Pterideæ. On general grounds it is most likely that *Platycerium* is related to the Matonineæ. Diels (4, pp. *336-337*) has placed *Platycerium* near *Cheiropleuria*, basing his comparison upon external resemblance, and Christ (3) groups these closely with *Dipteris*, a position which I am prepared to accept. But anatomically *Dipteris* is relatively simple; its simple solenostele is replaced by several concentric solenostelic cylinders in *Matonia*. In many other phyletic lines, it may be seen how the solenostele becomes broken into a dictyostele. It would be quite consistent with the structural facts here described, if we were to consider *Platycerium* with its complicated dictyostele as the dictyostelic type of a series of which *Dipteris* and *Matonia* are the solenostelic types. Any near relationship however, with these ferns, cannot be established solely on the basis of the anatomical results obtained so far, but with continued investigation of facts other than those of stelar structure, supported perhaps by the discovery of some intermediate types, the position of *Platycerium* will probably be found near to the *Dipteris-Matonia* series.

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INTERNATIONAL PHYTOGEOGRAPHIC EXCURSION (I.P.E.) IN AMERICA, 1913.

ONE of the most pleasing results of the International Phytogeographic Excursion in the British Isles organised by the British Vegetation Committee in 1911, was the enthusiasm with which the visitors from abroad decided to go and do likewise. The first outcome of these resolves has been the magnificent American tour of 1913, lasting two months (August and September), and attended by ten Europeans—Dr. H. Brockmann-Jerosch, Frau Dr. Marie Brockmann-Jerosch (Zürich), Professor Engler (Berlin), Dr. Ove Paulsen (Copenhagen), Dr. Edward Rübel (Zürich), Professor C. Schröter (Zürich), Dr. T. J. Stomps (Amsterdam), Mr. A. G. Tansley, Mrs. Tansley (Cambridge), Professor C. von Tubeuf (Munich).

The tour was arranged by Professor Henry C. Cowles (Chicago) and Professor F. E. Clements (Minneapolis), but owing to various circumstances the great bulk of the work of organisation rested on the shoulders of Professor Cowles, to whom the deepest gratitude of all the members of the party is due, not only for the completeness and perfection of the arrangements, but also for his unfailing kindness, good humour and self-sacrifice throughout the trip. Without these qualities in a leader, indeed, the best organised tour might well turn out unsatisfactory and even unpleasant.

Professor Cowles had two able assistants, Mr. George D. Fuller (Chicago), and Dr. George E. Nichols (New Haven), one of whom attended to the railroad tickets, and the other to the baggage of the party, but they by no means confined themselves to these very necessary tasks. Both were of the greatest assistance to the European visitors in the many unfamiliar situations incidental to American travelling, and both most substantially helped Professor Cowles to make the journey a profitable and pleasant one. Both Mr. Fuller and Dr. Nichols also took numerous photographs throughout the tour; and these will be available for members of the party, and will no doubt form a valuable record of the trip.

Besides the above-mentioned leaders, many American botanists joined the party for shorter periods; and indeed one of the pleasantest features of the tour lay in the numerous opportunities thus afforded to the visitors from abroad of making the acquaintance of their American *confrères.*

The arrangements of the organisers included the provision for members of the party of a pamphlet detailing the general arrangements of the tour (and incidentally furnishing a most useful guide to American travelling in general); as well as of a series of six sectional excursion programmes with full itineraries of each section, and excellent descriptions of the scenery and vegetation passed through by train or visited by the party.

The following notes do not, of course, profess to be in any way a complete record of the excursion; such a record would require indeed a considerable volume. They merely attempt to present an outline of the tour and such of the impressions of the present writer as may be conveniently set down in this place.

Most of the members of the party arrived in New York during the closing days of July, and made trips to the interesting "edaphic prairie" of Hempstead Plains in Long Island, and to the pine-barrens and salt marshes of New Jersey. The writer joined the party some days later at Chicago, and is thus unable to speak from personal experience of these excursions, but it may be stated that the New Jersey pine-barrens are of special interest to the European botanist, because they have much in common with European heathland. Dominated by *Pinus rigida*, with which are associated several species of more or less dwarf and scrubby oaks, forming a sparse and open woodland, the sandy soil is largely covered with a shallow dry peaty humus formed by *Cladonia*, and sometimes by species of *Polytrichum.* Species of *Vaccinium* and the closely-allied *Gaylussaccia* are also characteristic. On the whole, as in the case of the European heaths, the formation is, floristically, rather poor. In the depressions between the sand-ridges are "cedar-swamps" dominated by *Chamæcyparis thujoides*, in which occur *Sarracenia purpurea* and *Schizæa pusilla.* Professor Harshberger, of Philadelphia, was the principal leader.

In New York the party visited the unique Brooklyn Botanic Garden, the Botanical Department of Columbia University, under the charge of Professor R. A. Harper, and the New York Botanical Garden in Bronx Park, which bids fair to become one of the leading botanic gardens of the world. The Garden contains a tract of primitive eastern deciduous woodland, with a fine grove of hemlock spruce *(Tsuga canadensis)*; and the beautiful valley of the stream which traverses the Garden is skilfully utilised for the arrangement of the herbaceous beds. The water-loving plants are on the margin of the stream, and the xerophilous on the dry summit of the ridge close to some fine glaciated rocks, while plants of intermediate water preferences occupy the slopes between. The taxonomic affinities of the various families are brought out by the arrangement of the beds along the valley. Dr. Britton, the accomplished Director of the Gardens, and Mrs. Britton, so well known by their genial hospitality to botanists visiting New York, and Professor Harper, entertained the members of the party.

Leaving New York on the night of Wednesday, July 30th, the party made a stop at Niagara Falls on Thursday, and arrived at Chicago on the morning of Friday, August 1st. The international party was received by the staff of the well-known Botanical Department of the University, in the Botany Building, and afterwards entertained to lunch at the Quadrangle Club. Professor John M. Coulter, head of the Department, gave a short address of welcome, and then Professor Cowles delivered a short but exceedingly useful lecture on the physiographic and geological features of the Chicago region, indicating their relations to the vegetation and flora. The writer was amused by a remark made to him by an American botanist to the effect that whatever part of the United States one visited one was always told by the local botanist that this was a specially interesting region, because it was the meeting-point of two floras, the eastern and the western—or perhaps the northern and the southern—the obvious inference being that the conception of a "northern" or of a "western" flora gradually shifted as one moved south or east. There can be no doubt, however, as Professor Cowles insisted, that the Chicago region is, in a very real sense, the meeting-place of a northern and southern flora, and of an eastern and western vegetation. This means, of course, that there are actually a large number of species characteristic of the north or of the south which are found intermingled in this region, and that in Illinois and neighbouring States, the great eastern deciduous forest begins to give way to prairie.

One of the greatest attractions of the Chicago neighbourhood to the ecologist is, of course, the magnificent series of sand-dunes on the southern and eastern shores of Lake Michigan, and a large proportion of the week spent at Chicago was devoted to the vegetation of these dunes, already well-known to students of ecology from Professor Cowles' paper in the *Botanical Gazette* for 1899. An exceedingly useful pamphlet on "The Vegetation of the Chicago Region" was distributed to the members of the party, including a summary of the plant-associations with lists of species.

CHICAGO SAND DUNES.

The succession of plant-associations on the sand-dunes of the southern shore is very complete, well-marked and constant, leading from a beach association—very poor floristically like the maritime sandy beach associations of temperate regions in general, and including *Cakile* and such forms as *Corispermum hyssopifolium*, *Euphorbia polygonifolia*, *Cirsium Pitcheri*—through a fore-dune association characterized by sand grasses such as *Ammophila* and *Calamovilfa*, and by willows and sand-cherry, to a cottonwood association characterized by *Populus deltoides*, and occupying many of the large mobile dunes. From this point onwards the succession changes its character, owing to the protection from wind afforded on the landward side of the high mobile dunes; and the vegetation undergoes rapid stabilization and a subsequent succession. According to one American member of the party a sand prairie grass association in which the bunch grass (*Andropogon scoparius*) figures, can often be distinguished as the initial phase of this succession: the prairie grasses are quickly succeeded by pines (*Pinus strobus*—largely cut out on account of the value of its timber—and *Pinus Banksiana*, the dominant species), with which *Juniperus virginiana* and *Thuja occidentalis* are mingled. This pine-association has a very characteristic undergrowth of *Juniperus communis*, *Arctostaphylos Uva-ursi*, *Pyrola* spp., etc. Under the shade of this vegetation humus begins to develop in quantity for the first time. The pine-association soon begins to be invaded by the black oak (*Quercus velutina*), and a crowd of the less sciaphilous woodland shrubs and herbs. The pines are rapidly suppressed, and the typical black oakwood, often open, but in many places with a closed canopy, is established. This association forms a zone at least two or three miles wide in some places.

Here and there in the hollows are small lakes and marshes representing detached portions of "Lake Chicago" which have not been overwhelmed by the dunes, and showing all stages of succession from open water, through reed swamp, to an association of willows, etc., with other swamp-loving trees. Whether these areas ever become oakwood unless they are actually overwhelmed by sand is doubtful.

The black oakwood is often invaded by other species of oak, such as *Quercus alba* and *Q. rubra*, and thus passes to a mixed oakwood association with *Tilia americana*, etc., and many more shade-loving forms. Eventually this may be replaced, as is admirably seen at Sawyer, Michigan, by the typical shade trees of the north-eastern United States, dominated by the beech (*Fagus grandifolia*) and the sugar maple (*Acer saccharum*), with scattered examples or local groves of *Tsuga canadensis*, and such characteristic trees and shrubs as *Liriodendron tulipifera*, the papaw (*Asimina triloba*), the witch hazel (*Hamamelis virginica*) and the spice bush (*Benzoin æstivale*), etc., though some of these may occur somewhat earlier in the succession. The beech-maple forest shelters a typical shade-loving vegetation, with the beautiful and characteristic shade fern *Adiantum pedatum*, *Polystichum acrostichoides*, *Aspidium marginale* and *A. spinulosum*, and numerous angiospermous shade-herbs. There can be no doubt of the essential identity of this climax association of the sand-dune succession with the typical climax beech-maple forest of the neighbourhood as developed on clay soils.

Such a forest on glacial clay was visited near Three Oaks, Michigan, and though some of the species differ from those of the beech-maple forest on old sand-dunes, the essential identity of the vegetation in the two cases cannot be questioned.

MR. WARREN'S BEECH-MAPLE FOREST.

This beech-maple forest on clay is a magnificent specimen of virgin deciduous forest. The beeches and maples are about equal in numbers, and their tall finely-shaped trunks tower to a great height. One large maple measures 15¾ feet in circumference 2 feet from the ground. The shade cast is dense, and the evaporating power of the air very low. There is a typical shade ground vegetation with abundant ferns and many humus plants. The free rejuvenation of the dominant trees is a marked feature, a large proportion of the woody undergrowth being formed of young beeches and maples. In some places there is, I think, some evidence of differentiation of the ground vegetation by the local occurrence of more sandy soil. Round the shallow pools left in old "oxbows" of the river, such trees as *Platanus occidentalis* and the "soft" maple (*Acer saccharum*) occur.

This fragment of beech-maple forest is one of the few remnants of the magnificent deciduous forest that once covered nearly the whole of the north-eastern United States. Dr. Nichols informed us that the last remaining fragment in Connecticut was destroyed a year or two ago. The Three Oaks forest owes its preservation to the fine spirit of its owner, Mr. Warren, of Three Oaks, a feather-bone manufacturer. Mr. Warren originally bought the area for lumbering purposes, but was so greatly impressed by its beauty and interest that he has preserved it practically untouched, and is willing, we understand, to hand it over to a public authority, if guarantees can be obtained for its proper maintenance and preservation—a somewhat difficult matter. The members of the international party were delighted at having the opportunity of expressing to Mr. Warren's sons—by whom they were taken to and from the forest in automobiles, and afterwards most charmingly entertained at lunch at the Lakeside Club—their sense of the great debt of gratitude which not only botanists, but all lovers of untouched nature owe to Mr. Warren senior in this matter. The imagination and insight into the deeper æsthetic and indeed spiritual needs of the community shown by Mr. Warren are at present all too rare among the business men of any country. But we may confidently expect a time to come when education and greater leisure has raised the general demand for and appreciation of the glories of unspoiled nature. Future generations will be slow to forgive us for the wholesale and often wanton destruction that goes on at present almost unchecked by any general feeling that it is an antisocial crime, and quick to applaud the actions and to reverence the memories of those who have done something to preserve their heritage of natural beauty. No one but a fanatic, indeed, entirely out of touch with the realities of life, would expect to hamper the economic development of a great country, which necessarily involves the replacement of forest and prairie by corn-fields and factories. But here and there tracts of original untouched nature can and should be preserved for the enjoyment and use of our successors, without in any way checking general and inevitable economic development. This is work which ought to be undertaken by the community, and indeed the great national and the smaller State "parks" of the west—three of which were visited by the international party—are a sign that America is awake to her responsibilities to the future in this matter. In the east the work of preserving unspoiled areas is more difficult, and there is less opportunity for it because comparatively little original vegetation is left. All honour, then, to those few who have the insight and the generous spirit to subordinate motives of immediate material profit to higher and deeper considerations. Comparatively few may be found as yet to pay this honour, but those few will become many as time goes on, and the general level of appreciation of the permanent and underlying factors of human life in its widest sense is gradually, as it will inevitably, be raised to a higher and higher level.

Effect of Moving Sand-Dunes on Forest Vegetation.

All the stages of the sand-dune succession subsequent to the cottonwood stage are liable to be overwhelmed by moving masses of sand, 100 feet or so high, and the sequence of events that occurs when the later forest stages are thus invaded is most interesting. If the advancing face is moving at a comparatively slow rate, many of the trees and shrubs of the forest are not killed by the sand, but are able to grow up *pari passu* with the advance, and keep leafy shoots always above the surface, *e.g.*, species of *Rhus*, *Tilia americana*, *Prunus serotina*, *Vitis vulpina*, etc. This power depends upon the capacity to strike adventitious roots into the layer of damp sand which is found a few inches from the surface throughout the year. It is this capacity which enables the cottonwood (*Populus deltoides*) to dominate the less rapidly moving dunes. The seeds of this tree can only germinate in the very damp soil of the shallow depressions near the beach where the bottom water nearly reaches the surface, or in places with a similar soil-water content on the edges of pools. The seedlings can, however, hold their own by the rapid upgrowth of their shoots through successive layers of invading sand, into which, as soon as it becomes moist, adventitious roots are sent (provided, of course, that the onset is not too rapid); and thus many of the lower but still considerable dunes near the sea are loosely covered with flourishing cottonwood trees which started life at a level sometimes scores of feet below the existing surface. Where wind erosion has subsequently destroyed part of such a dune the eroded face shows the old stems and adventitious roots of the cottonwood at all levels.

When a large moving dune invades a forest belonging to one of the later stages of the dune succession, some of the trees, *e.g.*, *Pinus Banksiana* and *P. Strobus* are killed very soon; and neither the oaks nor the sugar-maple (*Acer saccharum*) can survive very long; but the trees and shrubs mentioned above maintain themselves by keeping pace with the rising sand. Accordingly we have the strange spectacle of the top of such a dune dotted over with perfectly healthy and vigorous examples of these trees and shrubs, representing the rejuvenated tops of individual members of a closed forest association buried many feet below the existing surface. None of these trees can, however, survive subsequent removal of the sand by wind.

EROSION OF DUNES.

Besides the constructive phases of the sand dune succession outlined above, the international party visited an example (at Michigan City) of erosion of forested dunes by wave action. Here the advance of the lake, by undercutting the base of the sloping sand cliff, was causing the sand to slip down the slope from the eroding edge of the forest floor, sometimes slowly and gradually, sometimes in considerable masses. Here and there large masses of sand holding the roots of great forest trees had slipped half-way down the sloping cliff, and the trees were still alive and in the erect position. In other cases, of course, the trees had collapsed altogether, and lay prostrate upon or at the base of the cliff. Parallel cases of the erosion of clay cliffs with the gradual destruction of the forest occupying the top of the cliff were observed at Lake Bluff, north of Chicago.

At this locality, too, a small sand-dune area with a somewhat different vegetation from that characterising the dunes on the southern shore of the lake was visited. Here the front of the dunes was occupied by a *Calamovilfa* association, closely resembling the *Ammophila* associations of European maritime dunes. Behind this was a belt of *Populus balsamifera*, which replaces *P. deltoides* here and there on the southern dunes and increases towards the north, and then came a narrow but very well-defined belt of *Juniperus horizontalis*, a very characteristic shrub, with horizontally-growing branches. associated with *Juniperus communis* (with its typical form and also a form close to *J. nana*) and *Arctostaphylos Uva-ursi*, together with a few examples of *Pinus Banksiana*. At the back of the dunes, where these abutted upon the clay cliffs, the oak forest of the cliffs had sent a fringe of deciduous trees, shrubs and woodland plants on to the sand. The shore erosion of the lake cut obliquely across the face of this little dune area; at the south end embryonic dunes were still forming, and following the shore northwards the erosion had reached successively older stages of the dune vegetation till finally it cut into the clay cliffs themselves.

OTHER TYPES OF FOREST.

In this neighbourhood the oak-hickory forest (*Quercus alba, rubra, velutina, macrocarpa, Carya ovata, Juglans* spp., etc.) on the clay cliffs was visited—quite a different type from the beech-maple climax forest already described. Here, however, the oak-hickory forest is regarded as the climax forest, the climatic region in which the beech-maple forest is the climax type having now been left. The trees on these clay cliffs are never very large or lofty, though the forest is mature.

The V-shaped ravines cut by small streams through these clay cliffs present an interesting and decidedly more hygrophytic type of vegetation, including such trees as *Acer saccharum, Tilia americana, Quercus rubra, Ulmus americana*; and such herbaceous plants as the handsome *Aralia racemosa, A. nudicaulis, Sanicula marylandica, Hepatica acutiloba, Thalictrum dioicum, Solidago latifolia*. This ravine forest is closely allied to the flood-plain and to the eastern climax types.

Another type of forest visited by the party during their stay at Chicago was the flood-plain forest developed along the damp river bottoms. This is a very characteristic type and quite rich floristically. *Salix nigra, S. amygdaloides* and *Populus deltoides* frequently fringe the river itself, and in the forest behind *Ulmus americana, Acer saccharum* and *Platanus occidentalis* are very characteristic, associated with *Fraxinus americana* and *F. nigra, Acer Negundo, Juglans* spp. etc. On the ground *Osmorhiza brevistylis, Cryptotœnia canadensis, Convolvulus sepium, Aralia nudicaulis, Sicyos angulatus, Campanula americana* and many other species occur.

This river-bottom type of forest is specially interesting because it is the type which extends, though greatly impoverished floristically, far to the westward into the region of climatic prairie, and indeed along the larger rivers right through the Great Plains region to the base of the Rocky Mountains. *Psedera* (*Ampelopsis*) *quinquefolia*, the "Virginia creeper," is ubiquitous in all these types of deciduous forest.

An interesting tamarack (*Larix laricina*) swamp, developed just behind the dunes, on the edge of an old river valley was visited on August 3rd. Here a succession can be traced from open water (perhaps an old hole in the river-bed that remained as a pond after the river was obliterated) of which practically nothing remains, through reed-swamp and sedge to tamarack wood. The centre of the swamp is now mostly occupied by an association of various species of *Carex*, including *C. filiformis* and *C. Pseudocyperus*, which are dominant. These are developed on a floating layer of peat through which rise numerous shoots of *Scirpus lacustris* and *Typha latifolia*, with here and there *Phragmites communis* and *Cladium mariscoides*, relicts of the former reed-swamp. *Lastrea Thelypteris* is very abundant on the peat, which has many of the characteristics of English fen. In places, however, bog plants such as *Sarracenia*, *Drosera* and others occur. A phase of shrubs (*Salix candida*, *Rhus vernix*, *Betula pumila*, *Rhamnus alnifolia*, etc.) leads on to the close canopy tamarack wood of *Larix laricina* and *Betula lutea* with *Acer rubrum*, *Nyssa sylvatica*, etc., and on the ground *Osmunda cinnamomea*, *O. regalis*, *Mitchella repens*, *Coptis trifolia*, *Trientalis americana*, etc.

This succession appeared to the European botanists to be essentially of the "Niedermoor" or fen type, with local tendencies only to develop a "Hochmoor" vegetation, as was seen in a neighbouring hollow dominated by *Chamœdaphne*. From descriptions however it would appear that some if not all of the more northern tamarack swamps arise from a "Hochmoor" succession.

CHICAGO PRAIRIE.

The Chicago region, as has been said, is naturally a region of mixed forest and prairie. To the east the eastern climax (beech-maple) type of forest predominated: to the west the prairie areas gradually increase, and the forest areas (oak-hickory type) decrease. The prairie shows several more or less distinct types, such as low prairie, blacksoil prairie, sand prairie and so on. Low prairie is clearly, in this region at least, a natural succession from lake and marsh or fen. Good transitional stages between fen and low prairie may be observed close to Chicago in the vicinity of Wolf Lake, and low prairie still exists within the city limits at Chicago Lawn. This contains, however, a good many species said to be typical of high prarie. Thus it is largely dominated by *Agrostis* with the ubiquitous *Poa pratensis* (called in America "Kentucky blue-grass") *Hordeum jubatum*, and *Elymus canadensis*. Among the species which clearly show the origin from fen and which are familiar to the European botanist are *Lathyrus palustris* and *Stachys palustris*; while *Spartina cynosuroides*, *Calamagrostis canadensis* and *Muhlenbergia racemosa* are low prairie grasses. Mixed with these are numerous Composites: *Liatris spicata*, *Aster multiflorus*, *Solidago rigida* and *canadensis*, *Erigeron ramosus*, *Rudbeckia hirta*, *Lepachys pinnata*, *Helianthus strumosus*, etc., etc. Among these are *Silphium laciniatum* (the well-known compass-plant), *S. terebinthinaceum* (prairie-dock), *S. integrifolium* (rosin-weed) and *Cacalia tuberosa* (Indian plantain) with their stiff conspicuous leaves. Other common high prairie species are *Potentilla canadensis*, the beautiful *Phlox pilosa* and *glaberrima*, *Petalostemum purpureum* and *candidum* (prairie clovers) and *Lobelia spicata*.

The prairies show several seasonal phases marked by the showy flowers of different abundant species which mature at different periods of the summer and early autumn.

The Chicago prairie is certainly a relatively stable plant-community, and some local botanists declare that its edges have shown no tendency to be invaded by forest for the last half-century. Professor Cowles, however, considers that on the whole it is probably to be regarded as a stage antecedent to forest. The Chicago region is physiographically very young, the low-lying land near the city and to the south-east having been comparatively recently exposed by the retirement of " Lake Chicago," the more extensive predecessor of Lake Michigan : and on general grounds it may well be that the succession of vegetation over the region as a whole has not yet reached its " climax type." In some places marsh or fen passes not into prairie but directly into forest. The factors which determine these different fates are not certain, but it is quite likely that they are due to the historical accident of the invasion of forest vegetation in one place and prairie vegetation in another, according to local proximity of the two parent types. When the prairie vegetation obtains a good hold of the ground, it would naturally greatly delay, even if it did not wholly prevent the invasion of forest.

START FOR THE WEST.

Taking leave of our kind hosts of Chicago, we left the city westward bound on the evening of Friday, August 8th, travelling straight through to Lincoln, Nebraska, where we arrived on the following morning. Through Illinois the characteristic oak-woods of the rising ground, largely dominated by *Quercus macrocarpa*, alternate with prairie in the depressions with black soil often derived from fen. The plain, however, is largely cultivated (maize, wheat, etc.) and the woods are mostly passing into a degenerate condition owing to their use as pasture grounds for cattle. The Mississippi was crossed after nightfall, and throughout the night we traversed the state of Iowa, a typical prairie state, now almost entirely under cultivation. In the daytime the journey across Iowa, at least by this route (the Burlington) is exceedingly monotonous. The gently rolling country is covered with a continuous succession of maize and wheatfields, with occasional pastured oak-wood on the higher ground, and no glimpse of untouched prairie can be seen. The oakwoods become rarer as the western boundary of the state, the Missouri river, is approached. The train crosses the river and runs northward along the west bank for some distance before Omaha, the largest city in Nebraska, is reached, and good stages of the development of flood plain-forest from sandbanks can be observed. The bluffs overlooking the Missouri, composed of loess, bear oak-wood.

On leaving Omaha, the plain, originally prairie, is now closely cultivated. The Platte river, one of the streams that come right through to the Missouri from the Rocky Mountains, is crossed and shows a narrow belt of fringing "river bottom" woodland.

At Lincoln the party was met by the veteran Professor Bessey, who had charge of the arrangements during the comparatively few hours we spent in that city. Thanks to the care with which Professor Bessey had planned the trip and to the generosity of the Commercial Club, which not only provided the whole party with automobiles, but also with an excellent luncheon at the clubhouse, we were able to use our limited time to the best advantage. We were also honoured by the presence of the Governor of the State and the Chancellor of the University of Nebraska, who were not only present at the luncheon but also accompanied the party on the automobile trip. The day was one of the hottest in the year, a shade temperature of 108° F. being recorded by the meteorological station in the afternoon. Thanks, however, to the automobiles and to provision of a shaded room at the club for resting during part of the afternoon, but little discomfort—except indeed from dust—was experienced.

LINCOLN PRAIRIE AND PLANTATIONS.

During the afternoon, several areas of rolling high prairie were visited, and these presented a striking contrast with the "low prairie" seen at Chicago. The high prairie grassland was dominated mainly by *Stipa spartea*; *Panicum scoparium* was locally dominant, and *Spartina michauxiana* on the lower-lying prairies. *Kœleria cristata* (agg.)—an extremely abundant grass throughout temperate North America—was also in evidence. Of conspicuous dicotyledons forming the typical prairie "societies" of Clements, there are the Leguminous species *Psoralea tenuiflora* and *esculenta*, *Amorpha canescens*, *Petalostemum purpureum*, *P. candidum*; and the Composites *Aster multiflorus*, *Solidago rigida*, *S. serotina* and *Vernonia fasciculata*, the last six species common to the typical climatic prairies of Lincoln and the far distant local prairies at Chicago Lawn. *Echinacea angustifolia*, the "Niggerhead," with its strongly convex almost black disc, is an abundant and conspicuous species.

The river-bottom forest fringing the streams is composed of *Ulmus americana*, *Acer saccharinum*, *A. Negundo*, *Quercus macrocarpa*, *Fraxinus lanceolata*, *Celtis occidentalis*, *Juglans nigra*, etc., with *Symphoricarpus racemosus*, *Ribes oxyacanthoides*, *Smilax hispida*, *Rhus Toxicodendron*, *Vitis vulpina*, etc., representing shrubs and lianes. Unfortunately, the examples of this association near Lincoln have all been pastured and the natural boundary between forest and prairie entirely destroyed. It is stated, however, from several different sources, that since the cessation of prairie fires, the forest steadily advances on the prairie where it has the chance, *i.e.*, where the tree seedlings are not eaten down by cattle. This fact however, scarcely justifies the view taken by one European member of the party, that the whole of the prairie is artificial and that its soil has previously borne forest! It is true that trees will grow, and grow well, when plantations are made on the prairie. We visited two plantations, one forty-four years old, composed of the western cottonwood *Populus Sargenti*, in which the trees were thirty to thirty-five feet high and in a flourishing condition. The soil of this plantation having been much trampled, bore mainly a grass vegetation, though three or four woodland plants had colonised it. But in the case of another plantation, the "Rogers woods," which was planted on the high prairie about thirty years ago, mainly with *Juglans nigra* and *Acer Negundo*, with some *Acer saccharinum*, *Ulmus americana*, *U. fulva*, *Fraxinus lanceolata*, and *Toxylon pomiferum*, the existing state of things is very striking. The two first-mentioned species are reproducing themselves freely, as also is *Ulmus americana*: *U. fulva* and *Fraxinus lanceolata* to a less extent. Seventeen other trees, shrubs and lianes have appeared, of which the great majority are native woodland forms; and at least thirty-six herbaceous species are now present, including ten woodland species. These data were very kindly collected for me by Professor Bessey, and afford a most interesting piece of information on the subject of the assimilation of plantations on non-forest soil to natural woodland types. To argue from facts of the kind mentioned to the startling conclusion that the whole of the existing prairies were once forest-covered is, however, scarcely legitimate.

In the near neighbourhood of Lincoln there are areas impregnated with salt, and these bear a specialised vegetation, which, according to Professor Clements, shows a well-marked succession from saline and brackish aquatic forms through *Salicornia* communities to communities of *Atriplex*, *Corispermum*, *Dondia* (*Suæda*) and *Salsola*. On the less salty portions of this basin, the party met several of the typical "shortgrass" plants of the Great Plains for the first time, such as *Bouteloua*, *Bulbilis* and *Grindelia*. These plants, presumably unable to endure the competition of the typical prairie species, colonise the edges of the saline areas, where many of the prairie plants cannot get enough water, just as they cannot in the climatically drier Great Plains.

In the late afternoon the party had the pleasure of visiting the Botanical Department of the University of Nebraska, and of listening to a lantern lecture by Dr. Raymond Pool on the sandhill vegetation in the north of the state, where there is an immense development of inland dunes. Dr. Pool, scarcely recovered from a very severe illness, laid the party under a deep obligation by his excellent account of this region, of which he has made a thorough study. A small example of the same type of vegetation was visited on the following day near Yuma, Colorado.

LINCOLN TO AKRON.

At six o'clock the party left Lincoln on their westward journey, delighted with their reception at the capital of Nebraska. The journey to Akron, Colorado, the next stopping-place, a distance of a little over 350 miles in a straight line, was made during the night, so that the transition between the Prairies and the Great Plains was not seen. As one travels westward the altitude gradually rises, from 1,148 feet at Lincoln to 4,650 feet at Akron and 5,183 feet at Denver, 15 or 20 miles from the foothills of the Rocky Mountains. The rainfall gradually decreases, from 27½ inches at Lincoln to 16 inches at Akron and 14 inches at Denver. These figures, however, give little idea of the actual aridity to the inhabitant of a country with a maritime climate like that of North-Western Europe, where the evaporation rate is very much lower. Most of the country near the railroad during the first part of the journey is cultivated, the chief crops being wheat, "corn" (maize), sorghum and alfalfa (lucerne), and very little prairie vegetation is seen. As the Great Plains region is entered the cultivation becomes occasional only, and the country is covered with the typical "short-grass" vegetation, having a totally different aspect from typical prairie. This is a grazing country, and "dry farming" unless with a considerable capital is a very precarious means of livelihood. The shortgrass vegetation is broken here and there by sand-hills which bear (strangely as it will seem to a European) a decidedly more luxuriant vegetation, akin to the prairie type, and largely dominated by bunch-grass (*Andropogon scoparius*). The small streams crossed are dry for a considerable part of the year and as one passes westwards into the Great Plains the fringing woodland gradually thins out and disappears, though the larger rivers which never dry up still retain it.

(*to be continued*)

HORTUS FLUMINENSIS: THE BOTANIC GARDENS OF RIO DE JANEIRO.

By R. C. McLean.

It was in accordance with an invitation very kindly extended to me by Dr. J. C. Willis, the present Director of the Botanic Gardens of Rio de Janeiro, that I set sail, at the beginning of October, 1912, for a country which I vaguely knew as very rich, and a visionary City Beautiful. In prospect, a voyage of 17 days seems somewhat formidable, but once accomplished it dwindles surprisingly in the imagination, and leaves one wondering why such voyages are not continually being made by European naturalists, when such rewards are bestowed upon all who accomplish a "sail to the su'thard."

We steamed slowly into Rio Bay in the glow of a red dawn; and, if there be any spectacle upon earth more glorious, it needs must, I fear, transcend the powers of human appreciation. For Rio is the Amazing City, and seems this morning, circled by fantastic mountains and deep forests, and lapped in pearl-pink mists, fit sea-capital for that legendary isle, whose name *Brazil* was given long ago.

The great bay—no river, in spite of the name—green, and island-studded, nearly landlocked too, save for the narrow gate where the towering Sugarloaf guards the way, stretches up some forty miles or so into the country, where, at the head of it, the Organ Mountains stand: but close by here, where lies the city, the quaintly shaped peaks crowd down to the very water edge; and in and out and roundabout among their foothills, twenty sprawling miles of it, lies the city among its palms, on the most extraordinary site for a metropolis that ever man chose.

Rio is a very large and splendid city, where one may obtain everything of the latest—at a price. It models itself pretty successfully upon Paris; and is perforce delightful.

There is unfortunately no University in Brazil as yet, but there is a celebrated School of Medicine in Rio itself, whence emanates most of the botanical interest in the country.

The Gardens lie in the southern outskirts of the city, some seven or eight miles from the landing-place, on a piece of level ground (a somewhat rare commodity hereabouts) between the peak of Corcovado and a wide lagoon; facing, not into Rio Bay, but towards the open Atlantic. As one approaches the Gardens, the first thing that appears is the line of giant West Indian Royal Palms (*Oreodoxa oleracea*) bordering the road. Passing in by the main entrance, one finds oneself facing along the famous central avenue of these Royal Palms, an avenue half-a-mile in length composed of individuals which are upwards of 150 feet in height. The effect of this gargantuan colonnade is unique, and somewhat overwhelming, but I cannot agree with the critics who find it displeasing. Its size is the saving grace of it, the one feature which no picture gives any true rendering of. This avenue traverses the main garden from North to South, and provides a magnificent *mise-en-scène* for glimpses of the mountains which rise all around. There are also two lateral avenues of the same order of size, all three meeting at the principal entrance.

A traveller's first impressions of a tropical garden are apt to be a little mixed, and depend, indeed, a great deal upon the sort of weather prevailing at the moment. If one's arrival at Rio be in the winter-time—any time that is, between April and September—the uppermost idea is likely to be astonishment, for here the newcomer finds a garden multitudinous with palms and epiphytes, yet an atmosphere so cold that he must wear English clothes or an overcoat, and keep all his flimsy tropical gear in the background. During the winter the climate resembles that of late spring in England. It is the dry season, the skies are clear, the sun is comparatively low and most vegetation passive; for Rio is 22½° S., and is only 50 miles within the Southern tropic. In September the rain begins to increase by periodical downpours, and every time the sun comes out it is a little stronger and a little hotter; while the hottest time of all, the height of summer, comes in January and February.

During the summer which is *par excellence* the rainy season, the sky is very often overcast and the air is extremely moist, yet for some obscure reason, even when the sun stands vertical in a cloudless sky it has nothing of its Eastern power. The sun-helmet is unknown—one can even spend an hour in the sun without any head covering at all, and escape unhurt—a luxury which those who know the torrid Indian suns appreciate immensely. Neither is the rain always like Eastern rain; quite uncommon are the torrents from the skies which destroy paths and plants together in a few hours: here is gentle English rain, even sunshine showers.

To find equatorial vegetation and a pure development of rain-forest at so great a distance from the Equator is indeed astonishing. The reason may be found in the local physiography—a low-lying, narrow, littoral belt, backed by high mountains, with a prevailing wind off-sea. The coast is perennially humid: whenever the wind blows off-sea it rains, whatever the season of the year may be, so that the weather is as incalculable as that of an English summer. The Equatorial current keeps the sea warmed for an abnormal distance south, and the effect of this upon the climate may be seen by a glance at any vegetation map of the world showing Drude's phytogeographic areas. Not only does the Tropical American region extend down to the Tropic of Capricorn, but it passes right out of the tropics altogether, and reaches as far as Porto Alegre and the Rio Uruguay, into a region that should be purely temperate.

Indeed, one of the finest and richest pieces of untouched rain-forest yet remaining in Brazil is found at Alto-da-Serra, between Sao Paulo and Santos, in a district actually south of the Tropic.

On the other coast of South America exactly the opposite climatic conditions occur, for the northward-moving Antarctic drift carries the temperate area right up into the Tropics themselves, and even under the Equator, torrid weather is not at all usual.

This piece of forest territory, which is now in the hands of the Government of the State of Sao Paulo, can be recommended in the very highest terms to any who wish to study true rain-forest. It is of wonderful richness, and, I am told, will compare favourably with anything in the Orient. All the well-known characters of jungle are developed abundantly. On the other hand it is very easily accessible, has a healthy, but very moist climate (with a rainfall of 3½ metres per annum) and there is available a comfortable and splendidly situated bungalow on the area. The ground has been for some years past the property and peculiar care of Herr von Ihring, director of the Sao Paulo Museum, who has cleared paths through the dense jungle, and projected other improvements.

But to return to the Botanic Gardens of Rio. They consist of two portions separated by a road. The one, much smaller portion, comprising about 14 hectares, lies between the road and the marshy edge of the Lagoa Roderigo da Freitas, and remains in a wild condition. The soil is wet and unsuitable for cultivation, but to the botanist the ground is equally interesting in its jungle condition, full of Bamboos and other moisture-loving plants. Big trees will not grow in this part of the garden, and the wood, though dense, does not stand much higher than in England.

The other area, the garden proper, contains about 27 hectares, being practically bisected by the main Palm Avenue. There is not very much open ground, for the marvellous collection of Palms gives rather a woodland aspect to the garden, an appearance which has been intensified by a rather too liberal planting of Mangos. These latter do not fruit in the Gardens, for the water-table is very near the surface, the level of the ground being only some 3-4 feet above the surface of the Lagoa, and the fruit-trees suffer from what planters call "wet-feet." Nevertheless they form very large and handsome trees. The great size which prevails among the trees, as compared with those of temperate climates, does not appeal to the observer immediately, but becomes impressed upon him gradually, An *Eriodendron*, 40 metres high and large in proportion, looks quite normal among its giant neighbours, and it is only after a little consideration of what a poor figure even a great English Elm would make by the side of it, that the huge stature of the tropical forest tree becomes apparent to the imagination. The last Director but one, Dr. Barbosa Rodrigues, was one of the greatest authorities upon the Palmæ. His library has just been purchased for the Gardens, and will form a valuable asset. The collection of Palms, which he was responsible for introducing into the Gardens, is undoubtedly the finest in the world—comprising nearly 400 species, represented by full-sized specimens in flourishing condition, which lend a charming grace to many of the views in which the Gardens abound. Indeed, from the spectacular point of view, it is scarcely to be believed that anything, in any country, can excel this combination of grand natural surroundings and cultivated beauty.

To realise the grandeur of these hills, the majesty of huge trees and quiet lawns beneath a torrid sun, or the multitudinous abundance of the lesser lives that fill every nook and cling to every crevice, such is the charm that the Gardens of Rio impress upon the minds of those who are happy to linger there.

Swift blaze of dawn, and sea-breeze in the palms, who can forget these things, once known, or the strong vocation that they lay upon him for ever? Or this broad-bladed grass, so painfully pricked-in, root by root, which forms such deep carpets, of purity incomparable, chosen playground of the host of sunny butterflies—all sorts and sizes, from the great *Morpho*, blue and ephemeral as a tropic wave, to the tiny "Figure of Eight" with its quaintly regular markings. Who was it called them "The Dancing Flowers"? Perhaps Lafcadio Hearn—I forget.

Or else this ceaseless wind among the leaves, irritating, perhaps, in the day time, if one be trying to photograph them on a slow plate, but taking on a deeper significance in the cool dusk, when only the winking fire-flies light the shadowy alleys of the trees, and the elfin piping of the tree-frogs welcomes in the night.

The rhapsodical view is apt to be partial, and while writing the preceding paragraph I forgot the mosquitos, which would never have happened in the Gardens themselves. Rio city itself is now wonderfully healthy, with a death-rate lower than that of many a European capital. Both yellow fever and malaria are ghosts of the past which have been laid, and, thanks to the very efficient sanitary service, the mosquito is almost negligible. But the Gardens do not come within the scope of the municipality's efforts, and, surrounded as they are by jungle, the mosquito remains and flourishes, uninfected fortunately, but capable of much minor mischief on its own account. Certainly anyone intending to penetrate into the forests near Rio, or anyone whose work will lead him to be out-of-doors after nightfall should neglect no safeguard against their incessant attacks.

Immediately behind the Gardens rises a hill some 300 feet in height, of which the slope lying towards the Gardens is included in their area. The remainder of these back-lying hills belongs to the

Horto Florestal, a Government institution designed to encourage the cultivation of certain useful plants. The forest on this slope, although not very rich in comparison with some Brazilian forest, has suffered no interference beyond the felling, in the past, of much of its big timber, a fate attending jungle everywhere within reach of human habitation. Nevertheless the timber is even yet heavier than that of many temperate forests, and the whole remains a perfectly presentable piece of tropical rain-forest. Its unique advantages of proximity to the excellent laboratories in the Gardens, enabled it to be used as the *locale* of experiments on certain ecological questions, the results of which will be published later. Although from the physiological point of view its floral diversity was not a matter of import, yet it is not very striking for a tropical forest, though greater than that of the average temperate woodland. There was little difficulty in collecting 50 species from among the ground herbs alone, and the total number of species present, even on this small slope, whose base might be a mile long, and its height perhaps 200 feet, cannot have been less than 300.

The trees are very diverse, but the area includes a specimen of an almost pure palm association (*Asterocaryum Ayri*) not a common phenomenon in tropical rain-forest, which is well-known to be characterised by the almost perfect commixture of its constituent species. For future students who wish to specialise upon forest however, Alto-da-Serra is certainly the spot to be recommended, after a stay in the Gardens has introduced them to the nature of the Flora. It is safe to say that no man living knows the Brazilian Flora in the way that we understand such knowledge in a temperate country. What such a feat would involve will be easily understood when the dimensions of the Flora are indicated.

Brazil is a country nearly as large as the whole of Europe, occupying almost exactly half of the continent of South America, and exhibiting every variety of climate and habitat, from these rain-forests to almost pure desert. Its vegetation has been as little altered by man as that of any other country of similar latitude in the world, except perhaps portions of Africa, and is of unsurpassable richness.

The Federal Area in which is situated the city of Rio is not large, say about as large as the County of London. A large part of it is covered by buildings, but such is the amazing diversity of form, that the *known* Flora of the remainder of this spot is estimated at not less than 11,000 species, and, considering the almost impenetrable nature of the forest, and the desultory way in which collecting is done, this figure cannot exhaust the possibilities. Indeed, any who are enthusiasts for the capture of undescribed species, may obtain them within a day's walk of the Gardens, in almost any direction.

With the same reservations as before in regard to completeness, the total Flora of Brazil is estimated at 42,000 species—including, not only the huge number in the "Flora Brasiliensis" of Von Martius, which is the basal work of reference, but also the large number variously published by independent collectors.

What riches a systematic exploration of the lesser known portions of Brazil would reveal, it is only permitted to man to dream. Still, it is possible that such an exploration may be commenced within the next few years, as the Brazilian Government is very creditably munificent in the encouragement of all attempts to open up the resources of their half-continent. The condition of up-country Brazil, even in the settled districts, cannot be called civilized, even by the most partial critic, and any such exploration would involve penetration into areas where the white man has never yet set foot, so that there are certain difficulties in the way of its accomplishment. "God is great," say the Brazilians, "but the forest is greater."

The forests upon the Rio hills are all rain-forests of the most pronounced type, and, where their timber trees have been cut, the lianes and climbing bamboos have multiplied to such an extent that a passage is very nearly impossible. "Matto" is the Brazilian name, and no word could be more excellently descriptive.

In such forest, an homogeneous formation, yet a pure mixture of the representatives of every order extant, where one can penetrate for a kilometre and hardly see the same species twice—the problems of transpiration and light supply are obviously dominant questions. The carefully-filtered light which eventually reaches the few Hymenophyllaceæ and Orchids on the ground, and the steamy air that rises through the tree tops, are the warrants for it; and some attempt was made to attack one or two aspects of these great problems during an all-too-short stay in Rio.

Not that forest is everything, even in the Rio Gardens. There are open spaces where European and Tropical flowers flourish bedded side by side as in an English Park: many also are the strange fruits which a visitor may enjoy if he be there in summer-time; but in these he will probably find disappointment, for tropical fruits do not seem to bear out their common reputation. Those of the sub-tropics are in general, more agreeable to an untrained palate.

The Gardens comprise, as above described, a considerable extent of uncultivated ground, of more interest to the botanist than to the general, but that is only a minor part of the total area, and the features of horticultural interest are many and striking.

Foremost in public estimation are the great Palm Avenues, but there are also plantations of Bamboos which reach a height of about 10 metres and form a water-side arcade, always in deep shadow; a group of *Dendrocalamus giganteus*, rivalling in size that at Peradeniya; an avenue of *Fourcroya*, striking too in its rigidity; avenues of Mangos; fine groups of the hugh musaceous *Ravenala madagascariensis;* a very good collection of Cycads—some 22 species—only just installed; sections devoted to distinctive families such as Aroideæ or Marantaceæ; a great abundance and variety of epiphytes on almost everything, even the telegraph wires being decorated, while some of the larger trees are hardly visible under their load of *Tillandsia*, *Rhipsalis*, Orchids, etc.; extensive nurseries; a collection of Conifers, including fine specimens of *Araucaria;* a pond full of Pontederiaceæ in variety, and many other aquatics; and, lastly, one must recall the great collection of Palms and the native trees, planted everywhere in great profusion.

The pond and its surroundings are remarkably picturesque, and, even on the hottest day the bamboo shade is cool. The water comes from a small river, running down the valley behind, and crossing the Gardens on its way to the Lagoa. From this river, higher up, water is led off into a canal, which passes along the hillside, and pours the water down into the Gardens in two cascades, from which it runs everywhere in little shallow waterways along the paths and among the grass.

There are three glass-houses in the Gardens, in cool spots, for the care of smaller and more delicate plants, and in one of these is housed a fine collection of Orchids, made by one of the naturalists attached to the Gardens, Dr. Armando Frazao, to whom I am very much indebted for his great kindness during my stay in Rio.

The Gardens contain some statuary, and also some fine old masonry, including a Colonial gateway, now almost unique. There is a bust of the Founder, Dom Joao VI, placed beside his great Palm brought from the West Indies, the mother-palm of all the *Oreodoxas* in Brazil; and there is also a rocky mound beside the pond which bears a monument to Fra Leandro, a churchly Director of a former day.

It is impossible to deny that the Gardens have suffered from past neglect, and there is a certain disorder that is indicative of the insouciant outlook of the Brazilian upon matters which do not concern politics; but even in the short time that Dr. Willis has been in office he has effected great improvements, and his energetic measures will within another year place the cultivation of the Gardens upon a very different footing.

Among other improvements at present in progress, may be mentioned the great expansion of the present small library, and the erection of a fine building for the accommodation of the herbarium, at present confined to a single room. The new library will then occupy the whole ground floor of the present single building which houses the executive offices, library and herbarium. These offices, the Director's present house, the Director's old house—a building dating from the XVIIth century, and now inhabited by work-people—and the laboratories, are all grouped at the western extremity of the Gardens, and are approached by a special gate from the Rua Jardim Botanico, which is rapidly being transformed from a country road into a broad Avenida.

The neighbourhood of the Gardens is interesting in itself. The brackish Lagoa Roderigo da Freitas between the Jardim and the sea, is but one of the many features of interest. Without doubt its plankton would repay investigation, so little being known about that subject in tropical countries. Upon the shore is an extensive stretch of Restinga forest, a type peculiar to Brazil, and ecologically uninvestigated. The valley behind the Gardens; the famous mountains themselves, all swathed in forest, and many another thing besides, the student can find to attract his attention. It is indeed to be hoped that many students will visit a tropical station of such merit. The general cost of living in Rio is undoubtedly high; but even a short visit repays one so amply, that this need not be an insuperable barrier; and accommodation at a moderate price can always be obtained without great difficulty. The journey can be performed without risk at any season of the year, but for a student the Long Vacation would be most convenient, and, by going out in May or even June, and returning in October, no outfit beyond ordinary English summer things would be needful, and tropical vegetation might be studied with the maximum of comfort.

THE BRITISH ASSOCIATION AT BIRMINGHAM.

Presidential Address.

FOR the first time in the history of the British Association, a woman was chosen as President of a Section, and in opening her address Miss Ethel Sargant referred to this innovation as an honour done to herself as a botanist and an act of generosity to her sex. Certainly the Section was amply rewarded by the admirable address in which Miss Sargant discussed "the development of botanical embryology since 1870"—a slightly misleading title, since the address was limited to Angiosperm embryology, though this is of course a sufficiently wide field. As was to be expected and desired, the President devoted a considerable portion of the address to the recent investigations on seedling structure and its interpretation, in which she has taken so large and notable a part.

The Problems of Angiosperm Embryology.

As pointed out by Balfour, embryology ought, strictly speaking, to deal with the growth and structure of organisms during their development within the egg-membranes before they are capable of leading an independent existence, but modern investigators have shown that such a limitation of the science would have a purely artificial character, and the term is now employed to cover the anatomy and physiology of the organism during the whole period between its coming into being and its attainment of the adult state. The older botanists used the term in its narrower sense, including the study of the embryo-sac and the structures contained in it before the formation of the unfertilised egg-cell as well as the fertilisation of the latter and its subsequent divisions, but they did not proceed beyond the resting stage of the embryo within the ripe seed. Here, as in Zoology, this division is arbitrary and inconvenient; hence in the following remarks embryology is taken to include every stage in the development of the plant from the first division of the fertilised egg-cell to maturity.

Systematists from Caesalpino onwards have paid much attention to the structure of the seed, and were indeed forced to study the embryo because its characters are often of systematic importance. Botanists became familiar with the structure of the embryo in the ripe seed before they had traced its origin from the fertilised egg-cell, or followed its development after germination. Since the early history of the embryo was a sealed book to observers without the compound microscope, work on the external morphology of seedlings preceded that on the formation of the embryo. In the school of seedling descriptive work the greatest name is that of Thilo Irmisch (1815-1879), whose work was neglected by the succeeding generation owing to the rapid development of microscopic botany, starting from Hanstein's classic work (1870) on the divisions of the fertilised egg-cell, which laid the foundation of botanical embryology in the narrower sense—the study of the embryo from origin to germination. The period in the plant's history beginning with the first division of the fertilised egg (a natural epoch, since a new generation dates from it) and ending with the formation of the ripe seed (a true physiological epoch, since it corresponds with a complete change in the conditions of life) would seem very well defined; but experience has shown that here, as in Zoology, embryologists lose more than they gain by dividing the subject in this way—one group of investigators beginning their work where the others end theirs—and that this division is neither so simple nor so natural as it appears at first sight. It is not simple because the embryo is not always completely dormant during the interval between the formation of the ripe seed and the first steps in germination. In most Monocotyledons and many Dicotyledons the embryo is an almost undifferentiated mass of meristem when the seed first ripens, and becomes differentiated internally and externally by degrees during the interval before germination : this is often called the maturation of the seed, and it is quite distinct from its ripening. Maturation is a process characteristic of the seeds of geophilous plants, which commonly lie in the ground for a year at least before germination; the embryo of such plants is not comparable morphologically with that in the seed of an annual which may have ripened at the same time, since the embryo of the annual has root, stem, and leaves besides its cotyledons, and is ready to germinate immediately on the return of spring. Hence the morphologist must continue his study of the geophilous embryo throughout the maturation period if he is to compare it with that of the annual ; even then he will find it less advanced than the annual embryo though both be examined as they break out of the seed, for the geophyte may, perhaps, be four or five years before it flowers, while the annual has to complete its whole life-cycle in a single season. The division of the subject into two parts, the first ending with the embryo in the ripe seed, is also an unnatural one, even if the time of maturation be included in that first period ; for the structure of the embryo cannot be completely understood by reference to its past alone. The observer must expect adaptive characters of three kinds :—(1) those imposed on the embryo in the past by its development within the embryo-sac while it is still parasitic on the parent plant ; (2) certain adaptations to the process of germination itself; (3) characters which will be useful after germination. Before the utility of these characters can be fully understood, the development of the seedling must be followed for some time. In short, the structure of the embryo is dependent upon its future as well as on its past, and a division of the subject which excludes that future is, as Balfour says, purely artificial.

The work done in recent years on the anatomy of the seedling has therefore not only completed Irmisch's work on its external morphology, but has also thrown light on the problems of early embryology, attacked by Hanstein and his immediate followers. These problems are of two kinds, relating to the internal anatomy and the external morphology of the embryo. Hanstein himself was chiefly interested in the former, and his work disposed once for all of the possibility that the embryo of Angiosperms might possess an apical cell in the earlier stages of its growth as a reminiscence of its cryptogamic ancestry. One general result of work on the embryo since Hanstein's time has been to discredit phylogenetic theories based on its early history; indeed, it was hardly to be expected that a small mass of meristem, developing within a confined space and feeding parasitically on the tissues of the mother-plant, should preserve ancestral features. Still, Hanstein and his successors did good service in elucidating the growth of the pro-embryo from the fertilised egg-cell; its division into suspensor and embryo; the general development of both, and the appearance of external and internal differentiation in the embryo before germination.

While some of Hanstein's general conclusions as to internal anatomy have become the common property of text-books—for instance, the early differentiation of the dermatogen and its subsequent development into the epidermal system—he was less successful in demonstrating the initial independence of plerome and periblem, and their relation to the vascular system of the mature stem. The early differentiation of plerome and periblem from the inner tissues of the embryonic axis and their continued formation at the growing-points of root and shoot are processes which demand the most careful investigation on account of their bearing on the stelar hypothesis.

Schoute's work on the exact relationship of plerome and periblem at the growing-point to the central cylinder and cortex as differentiated in the older regions of the same axis, whether stem or root, is very important. He accepts Van Tieghem's definition of the stele as the solid cylinder of root or stem enclosed within the endodermis. The endodermis itself is considered as belonging to the cortex because in the root its cells are opposite the radial files of the inner cortex, and indeed form the inmost rank of these files; this is assumed to indicate a common origin by repeated tangential division. The cells of the pericycle, the outermost layer of the stele, alternate with those of the endodermis. As a rule there is no corresponding radial arrangement in the cortical tissue of the stem, but where such exists (as in the stem of *Hippuris*) the endodermis is again included in it and terminates it. Schoute in 1903 got precise results in species of *Hyacinthus*, *Helianthus*, and *Linum*, in the roots of which the periblem passed into the cortex, its inner layer becoming the endodermis, and the plerome gave rise to the stele only; but owing to difficulties arising chiefly from the insertion of leaves close up to the stem apex and displacements in the original stem structure owing to this habit, Schoute found definite results only in *Hippuris*, where the plerome gave rise not only to the stele but also to the endodermis and to the two or three inner layers of cortex immediately beyond it. If Schoute's results are well founded the limit between plerome and periblem does not correspond with that between stele and cortex in the stem of *Hippuris*, and doubt is also thrown on the assumption made by all previous observers that rows of cortical cells arranged in radial files must be of common origin.

The stelar hypothesis is essentially an assertion of the real homology between the vascular systems of stem and root throughout all vascular plants. No difficulty arises so long as we are dealing with roots only, or with the stems of those vascular Cryptogams in which the vascular system is a closed cylinder without gaps at the insertion of the leaf-traces: in such plants the vascular cylinder is as well defined as in all roots and can be described in the same terms. But the case is quite different in the stems of Phanerogams, where apparently the primary vascular cylinder is a system built up of leaf-traces embedded in a parenchymatous matrix. The early anatomists were faced at once by this problem in its crudest form, for they began with the primary structure of the dicotyledonous stem, and that of the root was not clearly understood until many years later; since they attempted to interpret it by reference to the skeleton of the stem and in the same terms; though there is nothing in the anatomy of the root to correspond with the leaf-trace, and the leaf-trace is the vascular unit of stem structure in all Phanerogams. Even when the facts of root structure were accurately known, the conception of the leaf-trace bundle as the structural unit continued to be a stumbling-block. Modern anatomy dates from 1871, when Van Tieghem published the first of his series of memoirs in which the axial core of the root was treated as equivalent to the whole system of leaf-traces in the stem; a conception which gained ground from the first, and was popularised by the happy choice of the term "stele" in 1886. From that time the stelar hypothesis has replaced all other schemes of vascular anatomy; the advance then made on all previous generalisations has been shown by the new impulse given to research and the comparative simplicity introduced into text-book anatomy. It is generally accepted that the central cylinder of the root in Phanerogams is far more closely comparable to the leaf-trace cylinder of the stem than to any one of the traces within it, yet when the comparison becomes detailed difficulties arise. For instance, where there is a pith in the root it certainly forms part of the stele, which is a solid cylinder sharply defined by the specialised endodermis around it; but the leaf-traces in the young stem surround a massive cylinder of parenchyma exactly resembling the parenchyma of the cortex with which it is in apparent connection through the gaps between the leaf-traces. Even the secondary formations in the stem do not completely divide one system from the other; when a specialised endodermis is present it is not so clearly defined as in the root; in many cases it is not present, and in a few instances there is an endodermis around each leaf-trace. However, the stele in the stem of Phanerogams is not necessarily a morphological fiction because in many stems its precise limits cannot be determined, for morphology is not merely descriptive. If we suppose that the stem stele in remote ancestors of the Phanerogams was as well defined as that of the root, and clearly comparable to it, we may attach a real morphological meaning to the term when applied to modern Phanerogams, provided we can show cause to believe that what we call the stele in their stems represents the ancestral stele. Its tissues will then have a history distinct from those of the cortex, though not clearly separated from them. The burden of proof, however, lies with those who assert that an apparently continuous and uniform tissue can be separated into two parts of distinct origin.

The evidence advanced is of two kinds—one founded on the comparative anatomy of stems and the other on the history of the tissues of the individual plant. Schoute has collected evidence to show that in the stems of Angiosperms a specialised layer is commonly distinguished from adjacent tissues either by the peculiar thickening characteristic of the endodermis in the root, or by the presence of starch in its cells. He shows that such a sheath surrounds the vascular cylinder in a very large proportion of Dicotyledons and in a majority of the Monocotyledons, while among Gymnosperms it occurs but rarely; and since the Angiosperms in which this bundle-sheath is obscure or wanting are commonly closely related to species in which it is perfectly well-defined he concludes that its absence in such cases must be attributed to reduction. Allowing that such a layer is as general among Angiosperms as Schoute believes, doubt may still exist as to its homology with the endodermis of the root, which is defined, not only by its thickened walls, but also by the fact that the cells form the inmost rank of the series of radial files distinguishing the inner cortex, while in the stem the inner cortex cells are very rarely arranged radially.

As regards the second class of evidence, that drawn from the history of the tissues in the individual plant, we have already seen that the differentiation of plerome from periblem is far less definite at the growing-point of the stem than at the root apex, and doubts have even been thrown on the identity of plerome and periblem with stele and cortex respectively. But we must now follow the development of the tissues of the embryo into those of the seedling. The normal seedling of all Phanerogams consists at first of cotyledons, hypocotyl, and root, the plumular bud being still rudimentary. The hypocotyl is commonly the first part of the embryo to lengthen, and then its xylem is lignified a little earlier than that of the root or even of the cotyledon; but when, as in many Monocotyledons, the base of the cotyledon lengthens first, lignification begins in that region and advances through the hypocotyl to the primary root. The investigation of the anatomy of the seedling at this epoch becomes extremely important when the vascular system of the root is compared with that of the stem, for in the seedling we have a complete and simple vascular skeleton which at one end belongs to the primary root of the plant and at the other to its primary stem; hence there must be an intermediate region in which stem structure passes into root structure, and the method of transition should at least suggest, if it does not precisely determine, the relation in which they stand to one another. For this reason great value has been attached by anatomists to the transitional region of the main axis. Van Tieghem showed that there are several types of transition between root and stem, in all of which the xylem and phloem bundles of the root are continued into the cotyledons or plumule; on their way through the hypocotyl they may divide or be displaced, and the xylem bundles "rotate" (that is, they turn on their axes until the protoxylem is internal), but all the elements present in the root are continued upwards in regular succession and are simply re-arranged in the upper part of the seedling. Hence Van Tieghem considered that the steles of root and stem are completely homologous. Gravis and others, however, consider that there is no morphological continuity in the hypocotyl between the vascular systems of root, stem and leaf: their traces are merely in contact sufficiently intimate for physiological purposes, but there is no true homology between the central cylinder of the stem and that of the root. The third view is that of Chauveaud, who agrees with Gravis that the presence of external xylem is the rule in the hypocotyl and in the base of the cotyledon, but considers that this external xylem belongs to the primitive structure of hypocotyl and cotyledon as well as to that of the root.

As already stated, the vascular system of seedlings is first differentiated in the hypocotyl, base of cotyledon, and base of primary root. According to Chauveaud, in all these regions the primitive stele is root-like, the xylem alternating with the phloem and its development being centripetal; but this primitive formation is permanent only in the root and commonly in the lower part of the hypocotyl also—in the upper part of the hypocotyl and in the base of the cotyledons the first xylem elements are fugitive and disappear so early that as a rule they are missed completely by the anatomist, who is apt to prefer well-differentiated material and therefore to choose seedlings which are past their first youth. Chauveaud therefore considers that there is an early phase in the development of the seedling in which the stele of the hypocotyl—at that time the only representative of the stem—is developing on exactly the same lines as the stele of the primary root, and is, in fact, continuous with it. At that epoch each cotyledonary trace is also developing on the same plan: it belongs to the same phase of evolution. In many Dicotyledons the insertion of the cotyledons is the simplest imaginable—the original stele of the hypocotyl divides below the cotyledonary node and one half goes to each cotyledon. Where this formation is clearly developed there cannot be said to be any transition between stem and root structure, since stem stele and root stele are continuous and their steles are developing in the same way, while even the leaf-traces of the first two leaves are on similar lines, and their insertion therefore does not modify the structure of the stele. The structure we associate with the stem of Phanerogams appears as follows. In the transitional region of the hypocotyl the first xylem elements—perhaps only two or three at each pole—alternate with the phloem groups. The elements next differentiated lie within them, for development is still centripetal, but in two diverging groups. The xylem ray is then shaped like an inverted V. Each arm of the V approaches the adjacent phloem group as it travels inwards, until the last-formed elements lie on the same radius as the centre of the phloem group, but well within it. The next elements are differentiated on that radius, but are directed towards the phloem—development has become centrifugal. These successive xylem formations are termed by Chauveaud the alternate, the intermediate, and the superposed. The alternate elements are fugitive in this transitional region: they commonly disappear as the superposed elements become conspicuous. The intermediate xylem persists; but higher up in the hypocotyl the intermediate elements also disappear as the seedling becomes older. Hence in seedlings of a certain age we have endarch bundles at the top of the hypocotyl, forming a stele of the stem type, and an exarch stele lower down, which passes unchanged into the root, the connection between the two being maintained by the intermediate xylem of the transitional region.

Chauveaud believes the stem cylinder in the upper hypocotyl of a fairly old seedling to be a true stele, but one belonging to a later phase of evolution than that of the root, and not strictly homologous with it in the sense in which the earliest vascular formations in cotyledon and hypocotyl respectively were homologous with each other. He considers that the successive vascular formations—marked by the appearance of alternate, intermediate, and superposed xylem in turn—represent three successive phases of stelar development: the root stele corresponds with the first of these phases only. This implies the hypothesis that at some past period a group of plants in the direct line of descent of Angiosperms possessed a stele resembling that which is now a mere stage in the life of the individual; thus the alternate formation found throughout the very young seedling implies an ancestral group with an exarch stele in stem as well as root, and a leaf-trace of corresponding structure. If this view be adopted, the seedling must, during the period when it consists only of cotyledons, hypocotyl, and primary root, with the plumule present as a mere bud, represent a past period in race history when its ancestors possessed an exarch stele in both stem and root, when the stem stele belonged to the stem only and the insertion of leaf-traces hardly modified its structure, and when it entered the root without change, and therefore no transitional region occupied and puzzled the anatomist of the period! This early stage in the development of the seedling is succeeded by that in which the epicotyl (plumule axis) begins to grow, and as a rule the epicotyl is undoubtedly modern : its vascular skeleton is built up of leaf-traces which are endarch from the first, at the cotyledonary node they are inserted on the vascular cylinder of the hypocotyl which has become endarch at the top. This transition has been effected lower down in the hypocotyl, as described already, by the formation first of intermediate and then of superposed xylem together with the gradual disappearance of the original alternate xylem. Hence the cotyledonary node may be considered to mark the interval between two acts in the drama of evolution—an interval the length of which cannot be estimated, but is clearly to be reckoned in geological epochs. The race history of the phanerogamic stem-cylinder is at present unknown ; possibly the development of the hypocotyl may give a clue as suggested by Chauveaud, or Jeffrey may be right in deriving the leaf-traces from a simple tubular stele (siphonostele) which has become more and more broken up by the appearance of foliar gaps. Until this point is cleared up the exact relationship of the vascular cylinder of the stem to that of the root will remain obscure ; as a matter of convenience the stem cylinder will no doubt be called a stele, even should anatomists acknowledge that it cannot be considered as strictly homologous with the stele of the root, but much confusion of thought would be avoided if the two structures were not treated as strictly comparable.

Apart from the foregoing consideration of modern embryology in relation to a single problem of internal anatomy, namely, the comparison of the vascular system of the stem to that of the root, the evidence of embryology is of great weight in questions of internal morphology and phylogeny. Hanstein's account of the Monocotyledon embryo suggests two distinct problems : (1) whether a terminal member can be considered as a leaf, (2) whether Dicotyledons are derived from a monocotyledonous ancestor, or Monocotyledons from a dicotyledonous form. The most obvious interpretation of Hanstein's observations is that the single cotyledon of Monocotyledons is equivalent to the pair found in Dicotyledons: this would imply that Dicotyledons were derived from an ancestor with one cotyledon, apparently terminal, which gave rise to the existing pair by a process of splitting; but other interpretations are possible, and the terminal hypothesis received a shock when Solms-Laubach discovered that in certain Monocotyledons the single cotyledon is lateral from the first. The comparative antiquity of Monocotyledons and Dicotyledons has been one of the first questions raised by the study of seedling anatomy, and it is remarkable that both the hypotheses founded on work of this kind assert the greater antiquity of the dicotyledonous form; but if the cotyledonary member of Monocotyledons is derived from one or both cotyledons of an ancestral pair, it cannot be considered as terminal. Thus the evidence of seedling anatomy bids fair to settle both these problems, and probably others of the same kind.

Though the progress of botanical embryology has been here treated from the morphological side only, it is clear that every department of botany must deal with the immature plants as well as with the adult form. For instance, the struggle for existence between two species in any particular locality must be profoundly affected by the characters of their seedlings. If one species should gain a decided advantage over the other early in life, the vanquished species may never live to set seed, and may thus disappear from the neighbourhood in the first generation. This is an extreme case to show the importance of considering seedling structure in problems of ecology and distribution. The internal structure of seedlings is certainly a department of vegetable anatomy, just as their adaptation to the conditions of life is a department of vegetable physiology. That the connection between embryology and systematic botany must be equally close seems at first sight to be beyond dispute, but the exact nature of that connection is as yet undetermined. Certain features of the embryo are included among the characters used by systematists, but on the whole the latter have dealt exclusively with the adult plant, the embryo itself having been treated rather as a portion of the seed than as an individual. We need not be surprised if conclusions drawn from the new embryology—that is, the embryology which includes internal characters as well as external—sometimes appear to conflict with the results of systematic botany, and it does not necessarily follow that embryological evidence is of no systematic value. The fault may lie with the embryologists who, being human, do occasionally misinterpret their facts, or possibly the natural system may need some modification in the light of new knowledge. When both explanations have failed to account for the discrepancy in a number of cases, we may be forced to give up looking for phylogenetic results from embryology.

MORPHOLOGICAL AND PALÆOBOTANICAL PAPERS.

PROF. G. S. WEST read two papers on Green Algæ. In a paper on the structure, life-history and systematic position of the genus *Microspora*, he remarked that species of *Microspora* were among the commonest and most widely distributed of British freshwater Algæ, gave an account of the nature of the chromatophores in the various species, and pointed out that the structure of the cell-wall varied in the different species. The wall becomes disarticulated into H-pieces only in a few species. The zoogonidia are always biciliated, and their escape takes place either by disarticulation of the filament or by the rapid conversion of the cell-wall into mucilage; after a brief swarming they germinate at once and grow into new filaments. The formation of aplanospores was described, and also the germination of the latter. The systematic position of the genus *Microspora*, was discussed and it was suggested that it should be placed in the family Microsporaceæ of the Ulotrichales. In a paper (jointly with Miss Starkey) on *Zygnema ericetorum* and the genus *Zygogonium*, Prof. West pointed out that Kützing's genus *Zygogonium* was entirely synonymous with *Zygnema*, and that *Zygnema pachydermum* was merely a form of *Z. ericetorum*—so little different that it was scarcely possible to find a single discriminating feature. The conjugation of *Z. pachydermum* is quite like that of other species of *Zygnema*, and since the cytological structure of this Alga is absolutely indentical with that of *Z. ericetorum* it may be presumed that the latter also conjugates in a normal manner. It was suggested that the two figures given by de Bary in 1858 of conjugating *Zygogonium didymum* (= *Z. ericetorum* type), which have been used by Wille and others to uphold the retention of *Zygogonium* as a genus, were merely monstrosities. Nobody has ever seen such conjugation since, whereas the West Indian form of *Z. ericetorum* (described under the name of *Z. pachydermum*) conjugates normally. Hence the *Zygogonium* of de Bary and Wille must be dropped. All previous accounts of the cytological structure of the cells were found to be inaccurate.

Mr. S. P. Wiltshire described the biology of the apple canker fungus (*Nectria ditissima*), which is a genuine wound parasite. The normal reaction of the cortex to injury is the formation of a phellogen layer over the exposed area, and therefore inoculation can only be successful when the injury is deep enough for the fungus to reach the wood, otherwise the diseased portion is surrounded by the phellogen, the tree thus healing itself of the disease. The fungus travels across the cortex through the intercellular spaces, across the phloem and cambium by mechanically breaking through the cell-walls, and then traverses the woody elements and pith through the pits in the walls. The medullary rays do not form a special means of entrance to the wood. The reactions of the host against the disease are the formation of (1) phellogen, at the limits of the infected region in the cortex; (2) abnormal wood of cells very similar to those of the medullary rays and containing gum-sacs; (3) wound gum in the vessels, though this substance can be penetrated by the hyphæ.

Prof. A. H. R. Buller gave an interesting account of the hymenium in *Coprinus*, with special reference to the dispersal of the spores, and explained the remarkably effective mechanism by which the differing lengths of the basidia bring their spores to different levels on the surface of the gill and thus facilitate efficient spore shedding.

Dr. O. V. Darbishire described the development of the apothecium in the lichen *Peltigera*. Spermatia are very rare in this genus, being confined to a few species and even in these rather rare; yet in certain species apothecia are produced in great numbers. Fünfstück and Baur have investigated *Peltigera*, and without going into nuclear details Baur has described this as a case of apogamy. The author has found that the beginning of the apothecium occurs among the young marginal hyphæ of the thallus. Certain cells of the medullary hyphæ, which may be followed some distance back into the older parts of the thallus, swell up and stain more deeply than the others; they are at first uninucleate, but soon become multinucleate as they increase in size. Fusions with neighbouring cells are common, but no transference of nuclei has been observed. Soon there is a mass of closely interwoven cells full of cytoplasm and containing numerous nuclei; no coiled carpogonia can be made out, but taken as a whole these darkly stained cells can be seen to form part of a connected system of branched hyphæ coming from the medulla further back and passing into the cortical margin. The multinucleate condition is apparently due to simultaneous nuclear divisions in the cells, not to any passage of nuclei from cell to cell. When nuclear division is still active, long unbranched but multicellular hyphæ grow out towards the cortex, forcing their way through the latter generally at an oblique angle; these, which are from structure and appearance functionless trichogynes, gradually disappear. Certain of the larger cells—the "ascogonia"—now grow out, and the nuclei formed by simultaneous division (*i.e.*, female nuclei) pass into the ascogenous hyphæ, thus formed, in pairs. From these the asci appear to derive their first nucleus in the usual way.

Miss E. M. M. Hume, in a paper on the leptoids of *Polytrichum*, pointed out that these structures do not deserve the name of sieve-tubes in any ordinary sense of the word. Their contents differ from those of the other living cells in never including starch grains or large drops of oil, but each leptoid has a nucleus. They are rich in connecting threads, which are in the terminal walls and are also abundant in the lateral walls, especially thickly aggregated towards the ends of the cells. The threads occasionally show an arrangement into definite areas as in sieve-plates, but are more frequently quite diffusely scattered; where such plate-like areas occur there is no change in the thickness of the cell-wall. The area of the terminal wall is enormously increased by its bag-like shape, so that the end of one cell depends into the lumen of the next. The connecting threads do not differ in structure from those found in the cortical cells, and they do not appear to undergo any progressive change into slime strings, with accompanying alteration of the surrounding cellulose into callus. Histological arguments in favour of the conduction of organised food materials by the leptoids must be based upon the elongated shape of the cells, the great area of the terminal walls, and the wealth of connecting threads, especially aggregated towards the ends of the cells. From direct experiment, the conducting function of the leptoids seems, more probably, to be confined to albuminous materials and not to be concerned with carbohydrates. The latter are possibly conveyed by the hydroids, which probably have not a purely water-conducting function, Mr. R. C. Davie discussed the pinna-trace in the Filicales, and pointed out that there are two main types of vascular supply to the pinnæ—(1) the marginal type, occurring generally from leaf-traces which have no hooks at their ends; (2) the extramarginal type which appears regularly in connexion with leaf-traces possessing incurved hooks. The marginal type occurs, however, in *Aneimia* and in some species of *Dicksonia* in which the leaf-traces have more or less hooked ends. Variations of the usual methods of pinna-supply appear in *Loxsoma Cunninghami*, *Onoclea sensibilis*, *Hymenophyllum demissum* and *Nothochlæna affinis*, suggesting intermediate stages between the marginal and extramarginal types; while in some species of *Pteris* and *Hypolepis*, and in some of the Cyatheaceæ, there is a combination of marginal and extramarginal types. The supply to the ultimate pinnæ is always marginal, and the supply to the pinnæ in the earliest leaves is also marginal.

Dr. E. de Fraine described a new species of *Medullosa* from the Lower Coal Measures. The specimen consisted of a short length of stem surrounded by adherent leaf-bases, and of small size, the diameters of the transverse section being only 5 cm. × 1.5 cm., including the leaf-bases. The vascular system of the stem consisted in the upper sections of three irregularly shaped outer steles, roughly triangular in outline; one of these steles branched during the length of stem available, so that the lower sections of the series show a ring of four steles. The outer ring of steles encircles a small central strand or "star ring," which undergoes no change in the series and forms the characteristic feature of the fossil. A narrow zone of periderm enclosed the vascular tissues of the stem. The numerous leaf-traces passed out from the peripheral parts of the outer steles. The leaf-bases showed a typical *Myeloxylon* structure with numerous exarch collateral bundles and abundant gum-canals, and the hypoderma was of the *Myeloxylon Landriotii* type. In the general structure of the steles and of the leaf-bases, and in its histological details, the stem shows a very close resemblance to *Medullosa anglica*.

Prof. E. C. Jeffrey and Dr. D. H. Scott gave a brief account of certain Devonian plants showing structure. The specimens were collected in Kentucky and come from the lower part of the Upper Devonian, being therefore among the oldest known land-plants with their structure preserved. The forms investigated include *Calamopitys americana*, n. sp. (a stem allied to *C. annularis* and remarkable for the tracheid-containing pith and the paired leaf-trace bundles in the wood); *Kalymma* petioles (doubtless belonging to *Calamopitys americana* or allied species); *Calamopteris Hippocrepis* n. sp. (a petiole of the *Kalymma* group but with the bundles arranged in a horse-shoe form and largely fused); *Archæopitys Eastmani* n. gen. et sp. (a stem with dense secondary wood and numerous small mesarch strands of xylem scattered in the pith—probably one of the Cordaitales, allied to *Pitys*); *Periastron perfoliatum* n. sp. (a curious petiole with a median row of separate vascular bundles and large lacunæ in the ground tissue—allied to *P. reticulatum* Unger but whether a Pteridosperm or a Fern remains uncertain); *Stereopteris annularis* n. gen. et sp. (a petiole with a single large vascular bundle somewhat resembling that of *Clepsydropsis* or *Asterochlæna* in form but with solid wood and external protoxylem, cortex differentiated into several distinct zones); *Lepidostrobus devonicus* n. sp. (the oldest known fructification with structure, axis of an ordinary *Lepidostrobus* type, sporangia with usual columnar wall, spores in tetrads). The high organisation of these early land-plants is remarkable, considering how little is known of the higher terrestrial animals at this period. A full account of these fossils is to be submitted shortly to the Royal Society.

Mr. H. Hamshaw Thomas described a new type of Ginkgoalian leaf, from the Jurassic plant-bed of Cayton Bay, near Scarborough. These leaves are linear or oblanceolate in shape, with rounded or slightly bifurcated tips, short petioles, and dichotomising venation. The leaves are usually found in a mummified state; they can be readily detached from the rock, and yield beautiful cuticular preparations. The form of the stomata and subsidiary cells is very similar to that of other Ginkgoalian leaves, while they possessed the secretory tracts between the veins as seen in the modern form. The epidermal cells possess very characteristic papillæ. These leaves form the type of a new genus, *Eretmophyllum*, with two species, a second form having been found at Whitby. The specimens provide a further illustration of the importance of the Ginkgoales in the Mesozoic vegetation, while they are an example of the interesting preservation of some Yorkshire plants and of the importance of the study of cuticular structure.

Physiological and Other Papers.

Prof. J. Reinke read an interesting paper on "The Nature of Life." The veteran Kiel botanist protested against the view that life can be interpreted merely mechanically, and urged that the greater the progress in experimental physiology, the better we learn to use our knowledge of non-living matter for the explanation of the processes of life, the more we understand that a complete physicochemical analysis is impossible for any important life process. Behind all the physico-chemical facts ascertained by physiological studies there hides an unknown factor, "an x not be solved by levers and screws and chemical reagents." He maintained that although the laws of energy are valid in the organism as well as in unorganised nature, life being based on transformations of energy or "elementary processes," these processes are not thrown together without order in the living body, but are united by an invisible chain which maintains order among the elementary processes and represents the true difference between life and any event in lifeless nature. This "life principle" is, unlike the single elementary processes, inaccessible to physiological analysis; it is "no force or power, it is a princible of succession, of order, of regulation, of harmony."

Prof. W. B. Bottomley described investigations to show that ammonium humate can supply the nitrogen need of plants if soluble phosphates and potassium salts are present in the culture solution. Pure ammonium humate was obtained by abstracting bacteria-treated peat with distilled water, precipitating humic acid from the extract by hydrochloric acid, and after repeated washing of the humic acid adding just sufficient ammonium hydroxide to dissolve it. This was then diluted with distilled water in the proportion of 1 humate to 200 water.

Mr. W. Neilson Jones gave an account of some investigations on anthocyan formation, with special reference to the two following points. (1) When coloured petals of *Matthiola*, etc., are soaked in 95 per cent. alcohol they become colourless, when transferred to water they regain their original colour. It is believed that a pigment-producing mechanism and a reducing body are present in the petals. The amount of water in the cells determines which way the reaction shall go: in strong alcohol reduction occurs and the petals become colourless; in weak alcohol or water oxidation takes place, resulting in the production of pigment. It appears further that considerable quantities of reserve "raw material" occur in some coloured flowers, e.g., *Matthiola*, from which pigment can be produced. The darkening of flowers on fading is explicable on this hypothesis as being due to this raw material coming into action. (2) Benzidine gives a blue colour with a solution of oxidase. Methyl quinol gives no reaction with this oxidase solution alone, but on the addition of a trace of benzidine becomes oxidised to a red colour. Methyl quinol thus behaves towards benzidine as an epistatic member of a colour series (e.g., in *Primula sinensis*) to a hypostatic member—that is, it is able to manifest itself only if the hypostatic member is present. In this reaction the benzidine probably plays the part of a carrier of oxygen to the methyl quinol. Although it is dangerous to argue from analogy, in default of other evidence it would seem probable that the colours of an epistatic series are due to different substances behaving like the methyl quinol, rather than to the action of specific oxidases.

Dr. R. Ruggles Gates discussed certain cytological evidence to show that mutation and Mendelian splitting are different processes. Definite evidence has been obtained showing that some at least of the mutations of *Oenothera* are not due to recombinations of Mendelian characters, as various writers have assumed, but to irregularities in meiosis which lead to changes in nuclear structure. The only cases cited in the paper were those of *O. lata* and *O. semilata*, which offer a means of differentiating between characters inherited from the parents and those resulting from unequal or irregular chromosome distribution during meiosis. Miss Lutz and the author showed independently that the mutant *lata* has 15 chromosomes instead of 14, and along with Miss N. Thomas the author has recently found that the same is true of *semilata*, also that all individuals possessing the foliage and habit of *lata* or *semilata* contain 15 chromosomes, even when these characters are associated with others derived by inheritance from their parental forms. Thus in a mutating race of *O. biennis* from Madrid, one mutant was *O. lata biennis*, having *lata* foliage and *biennis* flowers; this plant has 15 chromosomes, and must have originated through a meiotic irregularity. Again, in F_2 of *O. rubri-*

calyx × *O. grandiflora* two individuals appeared in one family, having *lata* foliage and habit combined with *rubricalyx* pigmentation. This *lata rubricalyx* type also has 15 chromosomes, showing that in addition to the characters inherited from the cross, the *lata* foliage appears whenever the fertilised egg has 15 chromosomes. Such cases show definitely that mutation is a process which is independent of the combinations of characters such has occur in hybrids. The source of the 15 chromosomes was shown earlier to lie in occasional irregularities in the distribution of the chromosomes during reduction. In such cases two pollen grains of a tetrad receive 8 chromosomes and the other two receive 6. When an egg having 7 chromosomes is fertilised by a male cell from a pollen grain with 8, the resulting individual will have 15 chromosomes and the foliage of *lata* or *semilata*. The extra chromosome, which is a triplicate of a pair already present, is thus associated with the development of certain foliage characters in *Oenothera* in the same way that the accessory chromosome when present in duplicate is in certain insects associated with the development of female sex characters. This is the first case in plants in which a definite relation has been shown to exist between a chromosome and particular external characters.

Mr. A. S. Horne contributed some notes on variability in the flowers of *Stellaria graminea*. The diameter of the corolla in flowers belonging to individual plants of *S. graminea* varies from 4 to 15 mm., whereas it exceeds 20 mm. in *S. palustris*. The width of the petal segments may reach 0.5 mm., 2 mm., or intermediate measurements in *S. graminea*, but exceed 2 mm. and may reach 4 mm. in *S. palustris*. The stamens may be all very short (less than one-third the length of the sepals) and sterile, or all along (exceeding the sepals) and fertile, or of several intermediate types in *S. graminea*. The correlation between these characters was explained by means of a table. Plants were treated experimentally —transplanted, propagated vegetatively, and seedlings raised. In one experiment the flowers of a plant called B, with corolla diameter 14.5—15 mm., corolla lobe 1—1.2 mm., and stamens of the longest type, changed after 19 days to corolla diameter 6.4 mm., corolla lobe 0.7 mm., with stamens correspondingly reduced in size. Another form, A, with corolla diameter 9 mm., corolla lobe 1 mm., and stamens of intermediate type, remained unchanged. The experimentally produced flowers of plant B approximate closely to those of very small-flowered plants in nature.

Prof. F. E. Weiss gave an account of the phenomenon of juvenile flowering in *Eucalyptus globulus*. Some of the most striking cases of juvenile flowering were referred to, as for instance that of rose seedlings still in possession of their cotyledons and yet bearing a terminal flower on a stem only a few centimetres high. Several species of *Eucalyptus*, which show a marked difference between the foliage of the immature plant and the mature foliage, have been found in nature flowering on small shrub-like plants still possessing leaves of the immature type. A plant from Tasmania, described by Hooker under the name *Eucalyptus Risdoni*, was regarded by von Müller as only a form of *E. amygdalina*, differing from the latter only in the possession of broad sessile leaves of immature type; it has been suggested that the cool climate of Tasmania prevents this species of *Eucalyptus* from growing to proper vegetative maturity. Similarly *E. pulverulenta* and *E. melanophloia* seem to be juvenile flowering forms of *E. Stuartiana* and *E. crebra* respectively. The author described the occurrence of this phenomenon in *E. globulus*, in which it does not appear to have been formerly recorded. A young plant was cut down after its first year's growth to a height of about two feet. One of the lateral buds then grew out and became the leader, developing in autumn a number of flower-buds in the axils of leaves of the type usual in young plants, and these opened as flowers of normal size in June, when the plant was little more than two years old. Evidently *E. globulus* is capable under certain conditions of producing flowers on juvenile plants, such as occur in other species of the genus.

Prof. F. W. Oliver described the conditions of establishment of *Suæda fruticosa* and the manner in which this plant promotes the fixation of active shingle. He pointed out that while to some extent all shingle plants retard or modify the landward movement to which shingle beaches exposed to the sea are liable when very high tides are accompanied by onshore gales, *Suæda fruticosa*, owing to its shrubby habit of growth and high capacity for rejuvenescence, is the most effective stabiliser of all British shingle plants.

Miss W. H. Wortham discussed the origin and succession of the vegetation of the south-western corner of Anglesey, where sand-dunes form a spit about five square miles in area on a backbone of schistose rock.

Mr. P. H. Allen gave an account of a botanical survey of maritime vegetation at Holme, Norfolk, which has been begun by a party from the Cambridge Botany School.

The semi-popular lecture was delivered by Prof. W. H. Lang, who dealt with "Epiphyllous Vegetation." The lecturer described the conditions of life and the chief adaptations of the various algæ, lichens, and bryophytes which grow as epiphytes upon the leaves of arboreous plants and are chiefly found in tropical rain-forests. He pointed out the prevalence in such forms of an efficient means of attachment to the surface of the leaf, and laid stress upon the occurrence of flat disc-like early stages in the germination of the spores of epiphyllous liverworts as an adaptation to this mode of life. F. C.

NOTES ON RECENT LITERATURE.

THE HEMIBASIDII.

By A. W. Bartlett, M.A., B.Sc.

(1) Brefeld, O. "Untersuchungen aus dem Gesammtgebiete der Mykologie. Bd. xv. Die Brandpilze und die Brandkrankheiten." v. Berlin, 1912; pp. vi and 152.

(2) Rawitscher, F. "Beiträge zur Kenntnis der Ustilagineen." Zeitschr. f. Bot., Bd. 4, 1912, p. 673.

(3) Werth, E., and Ludwigs, K. "Zur Sporenbildung bei Rostund Brandpilzen." Berd. deutsch. bot. Ges., Bd. 30, 1912, p. 522.

(1) To the student of the Fungi the appearance of a fresh volume of Brefeld's "Untersuchungen" is always an event of importance. It is now more than forty years since the first volume was published, and the latest volume is the fifth one that has been devoted more or less exclusively to the Hemibasidii.

Chapter I. deals principally with the pathological phenomena which the "Smut-fungi" produce in their host-plants, and with the biology of the parasites themselves. It is mainly a summary of the investigations which the author has previously made, though numerous fresh observations are recorded. The author points out that the Hemibasidii are able to penetrate only into the very young tissues of the host, and that when the tissues have reached maturity they are quite inaccessible to the entrance of the parasite. The parts of a plant through which infection can take place may be grouped into three categories:—(*a*) the seedling in a very early stage of development; (*b*) the young pistil of the flower; (*c*) all the young growing-points of the roots, axes, leaves, flowers, etc., of the maize-plant alone may be infected by the spores of *Ustilago Maydis*. In the first case the infection is brought about by the sporidia produced by the chlamydospores, which germinate on the soil where they have fallen. In the second instance the chlamydospores are probably conveyed by the same means as are pollen-grains, viz., either by insects or by the wind, from an infected flower to the pistil of a healthy one, where germination takes place. The fungus enters the ovule, and the mycelium remains in the seed during its resting-period, and renews its growth only when the seed germinates, and it then finds its way into the growing-point of the stem. So a considerable period of time may intervene, as also in the first case, between the infection and the development of the chlamydospores in the flowers, leaves or other parts of a plant. Throughout this period, which may be a matter of several months, the mycelium of the fungus in the growing apex of the stem keeps pace in its growth with the growth of the plant, without betraying the smallest signs of its presence. No more perfect adaptation of a parasitic fungus to its host-plant is to be found in the whole vegetable kingdom.

The various Hemibasidii are passed in review, with the parts of the hosts where their chlamydospores are produced and the probable method of infection. By far the larger number develop their chlamydospores in some part of the flower of the host, particularly the ovary, but often in the stamens as well, and sometimes exclusively in the latter. Several species produce the chlamydospores in the tissues of the leaves or of the axis of the host-plant.

A peculiar phenomenon is observed in the diœcious flowers of *Lychnis dioica* and *L. alba* when they are attacked by *Ustilago Melandryi* [= *U. violacea* (Pers.) Tul.]. The anthers in the staminate flowers are filled with the blackish-violet chlamydospores. The pistillate flowers normally possess no stamens, but on plants infected by the parasite stamens are developed in these flowers and the anthers become filled with the spores. Thus, under the influence of the fungus the female flowers again became hermaphrodite.

Chapter II. deals with the perpetuation of the Hemibasidii both externally and within the host-plant. The chlamydospores are typical resting-spores, and by means of their thick, cuticularized cell-walls are well adapted to withstand unfavourable external circumstances. In fact the spores of many species will germinate only at the end of a long resting-period. The spores of several species were found to retain their viability for at least ten years, while the spores of other species show immediate germination but soon lose their vitality.

The perennation of the fungus frequently takes place within the tissues of the host-plant, principally in the subterranean axes, from which it passes each year into the growing points of the subaerial shoots. The mycelium may be best observed in the parenchymatous tissues of the nodes, and in the older nodes it is doomed to remain sterile. But if the top of the plant containing the fungus in the tissues of the growing-point be decapitated, the mycelium in the nodes then penetrates into the growing-points of the new shoots produced in the axils of the lower leaves, which take the place of the main axis.

A long-extended series of observations shows that, while in slow-growing plants, *e.g.*, *Primula officinalis*, the duration of the fungus in the annual shoots is assured year after year, the hyphæ are unable to keep pace with the extension in length of the shoots of plants of rapid growth, so that the fungus disappears after a certain number of years, and the plant finally becomes free from the parasite.

In Chapter III. Brefeld brings forward good reasons for removing from the Hemibasidii certain forms placed in this group on account of a superficial resemblance in the production of their chlamydospores, because the latter show striking differences in their germination from anything hitherto observed in the Hemibasidii. These doubtful forms are comprised in the genus *Geminella* (= *Schrœteria*) and among the root-parasites known as *Entorrhiza*, which are transferred to the Fungi Imperfecti. Also *Ustilago virens* (= *Tilletia oryzæ* Patouillard) when cultivated produced sclerotia, which on germination gave rise to ascocarps, very similar to those of *Claviceps*. On this account it has been assigned to the genus *Ustilaginoidea* belonging to the Hypocreaceæ.

Chapter V. is devoted to a consideration of the relationship of the Hemibasidii to the Basidiomycetes proper. An interesting new species, *Heptasporium gracile*, is described, the hyphæ of which show clamp-connections at all the septa, and bear numerous isolated, scattered basidia each producing five to eight, but most commonly seven, basidiospores. No other form of spore was discovered. Brefeld regards this fungus as a simple member of the Hemibasidii, which approaches the Tilletiaceæ on the one hand, and on the other shows a transition to the Autobasidiomycetes, as the simplest form of which it may be provisionally accepted. A similar fluctuation in the number of the basidiospores can be recognised in some of the lower Hymenomycetes, *viz.*, the Hypochnaceæ, and *Exobasidium.*

Finally, Brefeld surveys the occurrence of chlamydospores in both the higher and the lower Fungi, and points out the close agreement throughout in the conditions of their formation. A new species of *Chlamydomucor* — *C. macrocarpus* — is described and figured, which when grown in nutrient solutions, forms an abundance of large thick-walled chlamydospores in the course of its hyphæ to the exclusion of sporangia. But, when cultivated on a firm substratum, *e.g.*, bread soaked in beer-wort, the formation of chlamydospores is entirely suppressed. When the chlamydospores of *Chlamydomucor* are kept in a dry condition they are able to retain their power of germination for several months.

The occurrence of chlamydospores is a rare phenomenon in the Ascomycetes, but they are frequently found in the Basidiomycetes, especially in the Hemibasidii and Uredineæ, where they form a regular phase in the life-history. They reach their highest expression in the Uredineæ in which they exhibit three distinct forms. Although oidia are frequently found in the higher Autobasidiomycetes, chlamydospores are seldom met with. In one species, however, which Brefeld has named *Irpicium ulmicola*, there was an abundant formation of chlamydospores in the hyphæ forming the tissue of the hymenophore. The phenomenon of pleomorphy, so far as it is met with in the Basidiomycetes, is due principally to the production of chlamydospores.

(2) It has been shown by Dangeard,[1] Harper,[2] and Lutmans[3] that in several species belonging to both the Ustilagineæ and the Tilletiineæ the young spores possess two nuclei, while the mature spores are uninucleate; but the means by which the binucleate condition was brought about had not been ascertained. All three observers were of opinion that the fusions which commonly take place between the sporidia produced by the germinating chlamydospores are of a purely vegetative character. Federley,[4] however, claims to have seen in copulating sporidia the passage of the nucleus from the one cell through the connecting canal into the other sporidium, which he regards as a sexual process.

Rawitscher's researches were carried out principally with *Ustilago Maydis* and *U. Carbo.* In the former species no copulation takes place between the sporidia or the cells of the promycelium. The hyphal cells contain each a single nucleus. The binucleate condition arises by the disappearance of the transverse wall between two neighbouring cells of the hyphæ in the tissues of the host-plant, so that each young spore-producing cell comes to possess two nuclei. A fusion takes place later between the pair of nuclei resulting in the uninucleate chlamydospore.

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[1] Dangeard, P.A. "Recherches sur la reproduction sexuelle des Champignons." Le Botaniste, 1893, p. 240.

[2] Harper, R.A. "Nuclear Phenomena in Certain Stages in the Development of the Smuts." Trans. Wisconsin Acad., Vol. 12, pt. 2, 1899, p. 475.

[3] Lutmans, B.F. "Some Contributions to the Life History and Cytology of the Smuts." Trans. Wisconsin Acad., Vol. 16, pt. 2, 1910, p. 1191.

[4] Federley, H. "Die Copulation der Konidien bei *Ustilago Tragopogi pratensis.*" Finsk. vet. Vorhandl., Bd. 46, Heft 2, 1903-4, p. 1.

In *U. Carbo*, on the other hand, when several spores are germinating together an abundant copulation is observed not only between neighbouring cells of the promycelium, resembling the process of lateral conjugation seen in certain species of *Spirogyra*, but also between the cells of different promycelia. The sporidia also conjugate in pairs, or copulation takes place between a sporidium and a promycelial cell. Copulation is followed by the passage of the nucleus from the one cell into the other, so that the sporidia become binucleate, but no fusion of nuclei takes place at this stage. The sporidia germinate to produce a mycelium with binucleate cells, and all the cells of the hyphæ within the host-plant were found to contain two nuclei, as well as the young spore-cells. The mature chlamydospore, however, possesses but a single nucleus, so a nuclear fusion is inferred, although it could not be definitely observed.

If we compare the development of the two species of *Ustilago*, the principal difference between them consists in the fact that in *U. Carbo* the generation with paired nuclei preponderates over that with a single nucleus, while in *U. Maydis* the reverse is the case.

According to these observations, the Ustilagineæ in their nuclear behaviour appear to fall into line with the Uredineæ and the higher Basidiomycetes. The view first advanced by Brefeld, who suggested the term Hemibasidii, that the latter with their promycelium consisting of a variable number of cells and producing an indefinite number of sporidia, represent a stage in the evolution of the Eubasidii, where the basidium produces a small and definite number of spores, receives support from cytological evidence.

In their cytological as well as in their biological aspect, the Hemibasidii show the closest affinity with the Uredineæ, although a considerably more complicated life-history is often seen in the latter group. In both groups the promycelium arises from a chlamydospore (= teleutospore in Uredineæ) which is provided with a thick cell-wall and is often adapted to undergo a period of rest. The chlamydospore of both groups is binucleate in its young condition and uninucleate when mature. The origin of the binucleate condition by the copulation of two cells, not specialised for this purpose, is very similar in both cases.

Again, in the Eubasidii a fusion of two nuclei always precedes the formation of basidiospores, although this fusion takes place within the basidium itself, and not in the cell from which the basidium arises, as is the case when it is produced by a chlamydospore. But this is a detail of minor importance and does not interfere with the homology.

(3) Werth and Ludwigs describe briefly the development and germination of the chlamydospores of *Ustilago antherarum*, which does not appear to be a favourable subject for research. They were unable to confirm the early binucleate condition of the spores described by Dangeard.[1] They assert that when the sporidia conjugate, the nucleus does not pass from one cell into the other.

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[1] *Loc. cit.*

REVIEWS.

AN INTRODUCTION TO THE CHEMISTRY OF PLANT PRODUCTS:

By P. Haas and T. G. Hill. London (Longmans, Green & Co.), 1913; pp. xii and 401. Price 7*s*. 6*d*. Net.

WHILE it is generally admitted that a sound knowledge of chemistry and its experimental technique is an essential part in the equipment of the botanist, up to the present time there has not been available for English readers any single book presenting in a direct and readable manner the main facts in biochemistry of plants. This lack the authors of the work under review have successfully attempted to supply, inasmuch as they have brought together within the limits of a handy volume an extremely clear account, easily assimilable by botanical readers with even a relatively slight amount of chemical training, of the more important organic compounds occurring in plants, and of their physiological significance. The authors are to be congratulated on the happy result of their collaboration, for the dovetailing of the chemical and botanical sections throughout the book has been skilfully done, and these sections include much of the most recent work on such subjects as colloids and enzymes, as well as most of the recent important advances in the physiology of vegetable metabolism.

The book is divided into nine parts, dealing with (i) fats, oils, waxes, phosphatides; (ii) carbohydrates; (iii) glucosides; (iv) tannins; (v) pigments; (vi) nitrogen bases; (vii) colloids; (viii) proteins; (ix) enzymes. Under each heading the authors give a concise account of the distribution and occurrence of these substances in plants, their chemical and physical properties, methods of extraction, chemical and microchemical reactions, and significance in metabolism. The descriptions are not overloaded with references to literature, though the main sources of further information are indicated, and the material presented has been carefully and judiciously selected, much of the older literature dealing so largely with impure products having been wisely ignored. Doubtless owing to their anxiety to avoid the inclusion of statements based on quite recent work which may or may not be confirmed by future investigation, the authors have dealt with hardly any work published since 1910; for instance, the work of Sergius Ivanow on the metabolism of fats in higher plants, published in 1911 and 1912, is not mentioned in the book, though on p. 43, under the heading " Further References," a citation is given of his 1912 paper dealing with the synthesis of fats in the ripening of oily seeds. However, the authors have accomplished very successfully their difficult task of discriminating well established facts from statements requiring confirmation, and they have provided exactly what is required by the botanical reader—a direct and simple statement of the main facts concerning the nature and relationships of the various compounds built up and broken down in the course of metabolism in plants. The book ought to be used by all advanced students of both botany and chemistry, since it covers a more extensive field than any other work on vegetable chemistry published in English in recent years, and provides a compendium of information such as has hitherto been available only in the form of numerous separate monographs or in encyclopædias like those of Czapek, Wehmer, and Abderhalden, to mention only some of the recent biochemical compilations.

The book appears to be remarkably free from misprints, though "Priestly" occurs several times instead of "Priestley," and there are a few cases in which the same substance is given different names without any indication that these are examples of the richness of chemical nomenclature in synonymy—"orcin" and "orcinol" in successive paragraphs on p. 56, for instance. The book is exceedingly well got up, is published at an extremely moderate price, and will undoubtedly meet with a wide welcome as an indispensable work to all students of plant physiology.

F.C.

VEGETATION OF THE ENGADINE.

"Pflanzengeographische Monographie des Berninagebietes," by Dr. E. Rübel. Leipzig (W. Engelmann), 1912. Price 8 Marks.

THIS valuable and voluminous monograph may be taken as one of the best examples of an excellent series of works (1) on the vegetation of Switzerland by the phytogeographers of that interesting and beautiful country. The work is in two volumes, the first containing nearly 300 pages and the second rather more. The work begins with short accounts of the ecological factors, the climate, and the geological structure (by Dr. E. Blösch), and goes on to give a very full account of the vegetation. The second volume is of the nature of a Flora, and includes the mosses (by Dr. Th. Herzog), the lichens (by Professor G. Lindau), the fungi (by Dr. A. Volkart), and the plankton (by Dr. G. Huber). It will be seen therefore that Dr. Rübel has supplied botanists with a very comprehensive phytogeographical account of the Engadine.

This district is known to a not inconsiderable number of British tourists; and the writer had the pleasure a few years ago of being conducted by Dr. Rübel over many parts of the area. The Engadine is in the south-eastern portion of Switzerland, on the confines of Austria and Italy, and is one of the richest floristic grounds in Europe. The highest altitude reached in the Engadine is the summit of the Piz Bernina, 4,055 m. (13,300 feet), and the lowest—near Samaden—1,700 m. (5,580 feet). It will be seen therefore that the whole district lies in the sub-Alpine and Alpine zones.[1] The rainfall varies from 63 cm. (25 inches) at Belvoir, to

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[1] Wahlenberg's (1811) "lower Alpine zone" begins at 1,789 m., his "higher Alpine zone" at 2,112 m., and his "niveal zone" at 2,675 m., Christ's (1907) "zone of coniferous forests" begins at 1,800 m. (for northern Switzerland) and 2,100 m. (for southern Switzerland), and his Alpine zone at 2,700 m. (for northern Switzerland) and 3,000 m. (for southern Switzerland).

90 cm. (36 inches) at Pontresina, and 160 cm. (63 inches) at the Bernina Hospice—these being averages for five years.

The average snow-limit of the district is given at 2,960 m. (9,710 feet). The highest larch (*Larix decidua*) attains an altitude of 2,660 m. (8,730 feet),[1] and the highest Arolla pine (*Pinus cembra*) 2,580 m. (8,470 feet). The average dwarf-tree limit is put at 2,400 m. (7,870 feet), and the average tree-limit at from 2,200 to 2,250 m. (7,220 to 7,380 feet).

In addition to numerous excellent photographic illustrations of the vegetation, a beautiful coloured vegetation map accompanies the first volume, the colours being superimposed on the Swiss topographical map (1 : 50,000). As is well-known, these Swiss maps are perhaps the best in the world, as regards clearness, physiographical detail, and contouring. The maps of the Peak District—even the six-inch maps—compare most unfavourably with those issued by the Swiss authorities; and as I have recently worked with the British ordnance maps of the Peak District I may claim to know their virtues and their shortcomings.

Dr. Rübel's map is constructed on rather different lines from British vegetation maps. British vegetation maps are fully coloured: Dr. Rübel's map leaves the ice-covered areas and the boulder-covered areas uncoloured. However, as these areas are well depicted on the topographical maps themselves, there is no disadvantage in the plan adopted; and, besides, it materially reduces the cost of the map. Again, British maps reserve stippling for mixed or intermediate and transitional associations : Dr. Rübel uses stippling to indicate the chief forest trees. I am not convinced that this latter is the better course on the whole; but it has the advantage of permitting the indication, on one and the same map, of both the forest-trees and the ground vegetation.

The classification of the vegetation follows the well-known Swiss lines, as laid down by Professor Schröter. A number of "vegetation types" are regarded as the primary divisions; and these are successively divided into "formation groups," "formations," and "associations." The first four of the "vegetation types" are based largely on plant form, being (1) woods, (2) scrub, (3) tall herb ground (Hochstaudenflur), and (4) grass grounds (Grasfluren). The remaining "vegetation types" are determined more by habitat factors. The forest "formations" are dominated by (1) larch (*Larix decidua*), (2) Arolla pine (*Pinus cembra*), and (3) Engadine pine (*Pinus sylvestris* var. *engadinensis*, Heer[2]).

These forest or woodland "formations" are scarcely the "formations" of British phytogeographers. In the Engadine one finds, generally speaking, a continuous forest on the lower mountain slopes: there is a great deal of mingling of the larches and Arolla pines; and the Scots (or Engadine) pine is very local. The ground vegetation of the three forest types varies. That of the larch forest on the newer and fresher soils, is grassy: that of the forest of

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[1] The highest larch in Switzerland, according to Dr. M. Rikli, is in Valais, at 2,700 m. (8,840 feet).

[2] This variety is characterised by very short leaves, by the bark being red almost from top to bottom, by its yellow cones, and by its pointed crown. The habit of the tree allows a great deal of light to reach the ground. It is a very distinct-looking plant.

Arolla pine, on older and somewhat acidic soils, consists of heathy undershrubs; and that of the forest of the Engadine pine, on wetter soils, contains much *Vaccinium vitis-idæa*.[1]

The scrub "vegetation type" is divided into two "formation groups," (1) the tall scrub and (2) the low scrub. The tall scrub shows two formations, (1) the scrub of green alder (*Alnus viridis*) and (2) the scrub of mountain pine (*Pinus montana*). The green alder scrub occurs on the mountain slopes, prefers situations where there is a flow of water, and usually follows the streams. The soil is thus not only well-watered, but the water is well-aërated. The scrub is static; and, seen from the outside, it appears as a dense, dark green mass of high bushes with few or no shrubby or arboreal associates. The mountain pine scrub also occurs on the mountain slopes, but in drier situations. In the Pyrenees, it may be added, *Pinus montana* forms high forest; whilst in Austria, it is often a low gnarled shrub.

Of the low scrub (Kleinsträucher) "formation group," Dr. Rübel recognises two "formations," (1) the dwarf shrub (Zwerggestrauch) vegetation and (2) the espalier shrub (Spaliergestrauch) vegetation. The former is perhaps the most widespread of the plant communities of the Engadine, and is consequently very prominent on the vegetation map. It often covers the ground in the woods of Arolla pines, and sometimes in the green alder scrub and the scrub of mountain pine. It ascends higher than the present tree limit or dwarf-tree limit; and some Swiss plant geographers look upon its upper limit as indicating the former upper limit of trees. In this formation, Dr. Rübel distinguishes the following associations:—Rhododendretum ferruginei,[2] Vacciniëtum myrtilli; Callunetum vulgaris; Calamagrostidetum villosæ; Juniperetum nanæ; Arctostaphyletum uvæ-ursi. A community of *Vaccinium vitis-idæa* is placed as a sub-association (*Nebentypus*) of the Vacciniëtum myrtilli. The soil of this formation is shallow and acidic.

The espalier shrub "formation" of the Engadine is a low growing, light demanding, humus (acidic) demanding community which alternates with the dwarf-shrub associations. Dr. Rübel distinguishes an association of *Azalea procumbens* (with a sub-association of *Vaccinium uliginosum*), and an association of *Dryas octopetala*. Dr. Rübel would have liked to have found another term to designate this "formation," as *Vaccinium uliginosum* is a dwarf shrub and not an espalier shrub; but he has been unable to find a better word, and so continues to use this one known from Professor Schröter's works. The formation receives no special colour on the vegetation map.

[1] I have not noted any allusion to birch woods by Dr. Rübel; but there is a small community of *Betula pubescens* in the Val Roseg. During my short stay in the district, I only saw two plants of *B. alba* (*B. verrucosa*): these were near Pontresina.

It may be of interest to add that the following trees are dominant in types of forest in other parts of Switzerland:—*Quercus pubescens; Q. pubescens* and *Ostrya carpinifolia; Castanea sativa; Fagus sylvatica; Abies alba (A. pectinata); Picea excelsa* (2).

[2] *Rhododendretum hirsuti* occurs on calcareous soils; but such soils are rather of limited extent in the Engadine.

Passing over—for want of space—the extremely interesting "vegetation type" designated the tall herb ground (Hochstaudenflur), with its "formations" of "kar-herbage" (Karflur[1]) and "lair-herbage" (Lagerflur), we come to the "vegetation type" of grass grounds (Grasfluren). This is composed of the single "formation group" of grasslands (Wiesen), which is divided into three formations:—(1) manured grassland (Fettwiese), (2) moist grassland (Frischwiese), and (3) dry grassland (Trockenwiese). Here one may allude to the conflicting use of the terms Weide and Matte by different German-speaking phytogeographers. The Swiss (3) by Weide mean pasture or grazed grasslands; and by Matte they mean meadow or mown grassland. On the other hand, Professor Diels (4) by Wiese means grassland with tall herbage (4, p. 91), and by Matte he means grassland with low herbage (4, p. 96). Brockmann (5) makes several sub-divisions of meadow (Matte) depending on whether the manuring is regular or intermittent, whether the ground is sheltered or not, and whether the ground is siliceous or calcareous. Dr. Rübel describes in all twenty-seven "associations" of his three grassland "formations." Here he follows Brockmann (5) closely; and we may add that one of the chief points of Brockmann's monograph of the Puschlav region—which adjoins the Engadine—is its minute study of grassland "associations." Many of these, I suppose, would be regarded as "societies" by British plant geographers.

A group of Dr. Rübel's associations of moist grasslands deserves special comment, namely, the associations named snow hollows (Schneetälchen). This term was first used, and the communities designated by it, were first described by Oswald Heer. Schröter adopted the term, and described the community as an association. Brockmann raised the community to the rank of formation; and Rübel uses the term to cover a natural group of associations within the "Frischwiese." Warming (6, p. 319) refers to the community as the "snow patch flora." The ground of the "Schneetälchen" is gently inclined, flat, or concave; and is in spring and early summer saturated with water from contiguous melting snow. As may be inferred, the snow hollows occur in Alpine and Arctic regions. The soil consists of cold, wet humus. On siliceous soils, the associations recognised by Dr. Rübel are (1) Antheliëtum, (2) Polytrichetum, (3) Salicetum herbaceæ, and (4) Alchemilletum pentaphylleæ, whilst on calcareous soils, a Salicetum reticulati occurs. Three at least of these associations are British, one having been first described for this country by Dr. W. G. Smith (7) to whom it was pointed out on Ben Lawers by Professor Schröter and Dr. Rübel on the recent International Phytogeographical Excursion (1911).

Brockmann has shown that the members of the association have means (hairs, etc.) to prevent water from penetrating the tissues even when the plants are submerged in water for two or three weeks.

[1] "Kar" is an Austrian geological term to denote hollows dug out by glaciers. "Karflur" is a term introduced by Kerner to denote the tall herbage which often occurs in such places. The word "Kar" has been adopted by the Swiss, and seems to have no English equivalent. Hence my term "kar-herbage."

Rübel's fifth "vegetation type" is made up of swampy grounds (Sumpffluren), divided into two "formation groups," (1) "Hochmoor" associations (Hochmoorbestände) and (2) "Flachmoor" associations (Flachmoorbestände). The concepts of "Hochmoor" and "Flachmoor" have recently been discussed by Tansley (8) and Moss (9); and it is only necessary here to state that the "Flachmoor" of the Engadine would, very largely, be placed in the British moor formation and not in the fen formation, although of course in many parts of Switzerland, particularly in the lowland districts, true fen is largely developed. It may also be pointed out that one of Rübel's "Hochmoor" associations is dominated by *Pinus montana*, in the tree form, so that here, at all events, the determination of plant formations by plant form breaks down, as Dr. Rübel has two communities dominated by this species. The particular point has been discussed by Gradmann (10).

Dr. Rübel goes on to describe his sixth "vegetation type," the fresh water vegetation, and lastly his seventh "vegetation type," the stony grounds (Gesteinfluren). The latter are divided into three "formation groups," (1) rocky grounds (Felsfluren), (2) rubbly grounds (Geröll- and Schuttfluren), and (3) sandy and gravelly grounds (Sand- and Kiesfluren). The Felsfluren consist of a single "formation," namely, the Felsflur, the Geröll- and Schuttfluren of two "formations," namely (1) the fixed rubble (Schuttflur) and (2) the sliding rubble or screes (Geröllflur), and the sandy and gravelly grounds are represented by a single formation, namely, the alluvial ground (Alluvialflur). These include in all ten associations. It is worth while adding the special Swiss significance of a number of terms which are here used, taken from Schröter (11). "Blöcke" (boulders) are from 25 cm. upwards in diameter. "Geröll" refers to the sliding screes, "Schutt" to stones which do not move down the mountain side. "Kies," or gravel, refers to stones which are rounded by water action. Each of these—"Geröll," "Schutt," and "Kies"—may be "gross" or "fein." "Grossgeröll," "Grossschut," and "Grosskies" have stones with a diameter of 2·0—2·5 cm., whilst "Feingeröll," "Feinschutt," and "Feinkies" have stones with a diameter of 0·2—2·0 cm. The particles of sand are 0·025—0·2 cm. in diameter.

The second (floristic) part of Dr. Rübel's work is as important and as carefully done as the first; and it is worth while drawing special attention to the fact that in a large number of cases the altitudes reached by species are given, and that these altitudes are in numerous cases higher than any previously recorded.

Although the concepts of vegetation units in Dr. Rübel's monograph are not strictly comparable with those that are adopted in this country, it is obvious that they (the Swiss concepts) serve quite well to describe the vegetation of the mountainous districts of Central Europe; and I have purposely refrained from any criticism of the Swiss views. The time is not ripe for a settlement of the vexed questions which are involved. It is my strong opinion that what is needed at present is not controversy, but a thorough understanding of each other's point of view; and if this review has been of a rather formal character, my excuse is that I wished to give some assistance to the younger and more serious-minded British ecologists in their efforts to become familiar with the phytogeographical work of recent Swiss phytogeographers. As for rival schemes for the expression of the facts, it is certain that in the end the fittest scheme will survive; but there is, in my opinion, no hope that the process of the elimination of the unfit schemes will be completed during the life-time of the present generation of ecologists.

Dr. Rübel's monograph concludes with a long list of references to the literature cited in the work, and with a full index.

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C. E. MOSS.

R. Madley, Steam Printer, 151, Whitfield Street, Fitzroy Square, London, W,